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The effects of body size and environmental temperature on locomotor efficiency were examined for the bottlenose dolphin (*Tursiops truncatus*). Because dolphins rely on limited on board energy supplies during submergence, they represent ideal models for assessing mechanisms of fuel efficiency for autonomous underwater vehicles. This study found that submergence could be prolonged by 1) packaging of energy stores based on body size, 2) opportunistic use of hydrostatic pressure to reduce stroke frequency, and 3) delaying thermoregulatory (maintenance) costs. These findings provide new insights regarding mechanisms for improving locomotor efficiency in large aquatic vehicles, particularly for deployment in extreme environments

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FINAL REPORT

GRANT NUMBER: N00014-96-1-1023

PRINCIPAL INVESTIGATOR: Terrie M. Williams

INSTITUTION: University of California, Santa Cruz

GRANT TITLE: The Effects of Body Size and Environmental Temperatures on Swimming Efficiency in Marine Mammals: Guidelines for Novel Underwater Propulsive Systems

AWARD PERIOD: 1 May 1996 to 30 April 1999

OBJECTIVE: To define the morphological, physiological and environmental limits of propulsive efficiency in cetaceans.

APPROACH: The effects of body size and environmental temperature on aerobic capacity were investigated for a representative elite diving marine mammal, the bottlenose dolphin (*Tursiops truncatus*). Evaluations of physiological responses and performance capabilities were conducted for animals in controlled conditions in pools (Long Marine Laboratory, UCSC) and during trained ocean dives at the U.S. Navy Marine Mammal Laboratory (SPAWAR, San Diego) and the Dolphin Experience (Freeport, Grand Bahama Island). In addition, comparative studies were conducted opportunistically on large and small species of cetacean at marine mammal parks and aquariums. Relative size of oxygen stores in the muscles, blood, and lungs of odontocetes and a mysticete were also evaluated from tissue samples and from previously published values in the literature. Aerobic dive limits for cetaceans were calculated from these data.

Laboratory measurements included voluntary breathhold duration, and changes in blood gases and lactate with apnea. These were assessed with respect to body morphology and on board oxygen reserves to determine the effects of body size on energetic reserves for aquatic propulsion. Open water experiments included an assessment of sprint and routine speeds during diving and swimming, which were examined using miniaturized instrumentation packs, underwater videography and SCUBA divers. Skin temperature and surface heat flow during rest, swimming exercise and diving were also determined for open ocean trained dolphins. These data were subsequently used to determine the relationships between water temperature, locomotor efficiency, and submergence time for this species.

ACCOMPLISHMENTS: The graduate students supported in this grant successfully completed laboratory and field studies concerning the mechanics, physiology and thermoregulation of bottlenose dolphins. In the laboratory setting muscle oxygen stores in the form of myoglobin were determined for cetaceans ranging in size from the 70 kg

common dolphin to the 80,000 kg bowhead whale. Myoglobin content and body mass were both positively correlated to maximum dive duration for cetaceans. Bottlenose dolphins demonstrated myoglobin levels that were on the low end of the range despite an intermediate body size and capacity for diving.

Thermoregulatory capabilities of resting, swimming and diving dolphins were examined for three adults acclimated to warm water conditions (Twater = 28.6°C) during four different field trips. By examining heat flow and skin temperature for one central and two peripheral anatomical sites, thermal windows for dolphins were identified. Heat flow from peripheral sites (dorsal fin and fluke) increased over resting values immediately after swimming exercise and required over 20 minutes to return to baseline levels. Cardiovascular changes associated with submergence affected heat flow during diving. The result was a reduced capability for heat dissipation until post-dive surface periods.

In addition to the physiological responses of dolphins to submergence, physical changes with depth appeared to influence locomotor activity patterns in this species. By evaluating the stroke frequency, and stroke amplitude of diving dolphins, this study demonstrated a key energy savings mechanism for dolphins, passive gliding. Changes in buoyancy associated with hydrostatic pressure at depth initiated the switch in level of swimming propulsion. Videotapes from hand-held submersible cameras and from miniaturized instrumentation packs placed on trained, deep diving dolphins revealed prolonged periods of passive gliding. The use of gliding, burst and glide, and constant stroking correlated with the depth and phase of the dive. By modifying locomotor patterns to account for the changes in hydrostatic pressure with depth, bottlenose dolphins were able to conserve limited oxygen stores during submergence.

Three Master's theses were completed using these data.

CONCLUSIONS: Based on these studies, we identified three major adaptations that facilitate locomotor efficiency in large aquatic mammals. These include
1) improved packaging of energy stores both in terms of size and quality of reserves (Noren and Williams, 2000)
2) opportunistic use of hydrostatic pressure to reduce stroke frequency in diving dolphins (Skrovan *et al.*, 1999)
3) conservation of energy reserves by delaying thermoregulatory costs during submergence (Noren *et al.*, 1999).
Overall, we found that the swimming efficiency of bottlenose dolphins, as for other marine mammals, was constrained by the physiological building blocks associated with a terrestrial ancestry (Williams, 1999).

SIGNIFICANCE: These studies in conjunction the parent grant have provided new insights regarding mechanisms for improving locomotor efficiency in large aquatic vehicles, particularly for deployment in extreme environments. The comparison of aerobic stores in large and small cetaceans demonstrated that both size and quality of energy reserves are important. Two important mechanisms for conserving limited energy

stores, delaying maintenance functions and taking advantage of changes in hydrostatic pressure to turn off propulsive systems, have direct application to duty factors used with autonomous underwater vehicles. In addition to biomimetic applications, these results provide information useful for the husbandry and deployment of animals in the U.S. Navy Marine Mammal program.

PUBLICATIONS AND ABSTRACTS (for total period of grant):

Publications
1. Noren, D.P., Williams, T.M., Berry, P., and Butler, E. 1999. Thermoregulation during swimming and diving in bottlenose dolphins, *Tursiops Truncatus*. J. Comparative Physiology B 169: 93-99.

2. Noren, D.P. 1997. Balancing the conflicting physiological demands of thermoregulation and diving in the Atlantic bottlenose dolphin, *Tursiops truncatus*. Master's thesis, UCSC.

3. Noren, S.R. 1997. Oxygen stores and acid base buffering capacities of cetacean skeletal muscle: A hierarchy in adaptations for maximum dive durations. Master's thesis, UCSC.

4. Noren, S.R. and Williams, T.M. 2000. Body size and skeletal muscle myoglobin of cetaceans: adaptations for maximizing dive duration. Comparative Biochemistry and Physiology A 126, 181-191.

5. Skrovan, R.C., Williams, T.M., Berry, P.S., Moore, P.W., and Davis, R.W. 1999. The diving physiology of bottlenose dolphins, (*Tursiops truncatus*) II. Biomechanics and changes in buoyancy with depth. J. Exp. Biol. 202: 2749-2761.

6. Skrovan, R.C. 1998. Biomechanics and changes in buoyancy with depth in diving bottlenose dolphins, *Tursiops truncatus*. Master's thesis, UCSC.

7. Williams, T.M. 1999. The evolution of cost efficient swimming in marine mammals: Limits to energetic optimization. Phil. Trans. R. Soc. Lond. B 354, 193-201.

Abstracts
1. Noren, D.P. and Williams, T.M. 1996. Balancing thermoregulation and exercise demands during diving in the Atlantic bottlenose dolphin, *Tursiops truncatus*. The physiologist 39 (5): A28.

2. Noren, S.R. and Williams, T.M. 1996. The relationship between muscle oxygen stores and maximum dive durations in cetaceans. The Physiologist 39(5): A28.

3. Skrovan, R.C. and Williams, T.M. 1996. Intermittent propulsion as an energy conserving mechanism for diving mammals. The Physiologist 39(5): A62.

4. Williams, T.M. 1999. Sink or swim strategies for low cost diving in marine mammals. American Zoologist 39(5): 4A.

5. Williams, T.M. and Hurley, W.C. 1999. Batteries not included: Marine mammal strategies for cost efficient underwater performance. Proceedings of the 11th International Symposium on Unmanned Untethered Submersible Technology (99-8-01).

The evolution of cost efficient swimming in marine mammals: limits to energetic optimization

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Mammals re-entered the oceans less than 60 million years ago. The transition from a terrestrial to an aquatic lifestyle required extreme morphological and behavioural modifications concomitant with fundamentally different locomotor mechanisms for moving on land and through water. Energetic transport costs typically reflect such different locomotor modes, but can not be discerned from the fossil record. In this study the energetic challenges associated with changing from terrestrial to aquatic locomotion in primitive marine mammals are examined by comparing the transport, maintenance and locomotor costs of extant mammals varying in degree of aquatic specialization. The results indicate that running and swimming specialists have converged on an energetic optimum for locomotion. An allometric expression, $COT_{TOT} = 7.79 \text{ mass}^{-0.29}$ ($r^2 = 0.83$, $n = 6$ species), describes the total cost of transport in $J \text{ kg}^{-1} \text{ m}^{-1}$ for swimming marine mammals ranging in size from 21 kg to 15 000 kg. This relation is indistinguishable from that describing total transport costs in running mammals. In contrast, the transitional lifestyle of semi-aquatic mammals, similar to that of ancestral marine mammals, incurs costs that are 2.4–5.1 times higher than locomotor specialists. These patterns suggest that primitive marine mammals confronted an energetic hurdle before returning to costs reminiscent of their terrestrial ancestry, and may have reached an evolutionary limit for energetic optimization during swimming.

Keywords: swimming; energetics; transport cost; marine mammals; locomotor evolution

1. INTRODUCTION

The evolutionary pathway of marine mammals involved transitions from terrestrial specialists to intermediate forms capable of moving both in air and water, and from these intermediate forms to aquatic specialists (Repenning 1976; Berta *et al.* 1989; Thewissen *et al.* 1994). These transitions were associated with morphological, physiological and behavioural modifications to overcome the disparate physical demands of locomotion through two different media. Since water is 800 times denser and 60 times more viscous than air (Dejours 1987) the transition from terrestrial to aquatic locomotion undoubtedly challenged the mechanical and physiological systems of ancestral marine mammals.

Many of the morphological transitions that led to proficiency in the aquatic environment are revealed in the fossil record. Fossil cetaceans (*Ambulocetus natans*) and pinnipeds (the Enaliarctidae, *Potamotherium*) demonstrate transitional forms within these lineages (Repenning 1976; Berta *et al.* 1989; Thewissen 1994; Thewissen *et al.* 1994) and reflect a continuum for locomotor optimization in marine mammals. Common to these ancestral marine mammals was a locomotor apparatus that supported movements on land and in water. For example, the limbs of transitional pinnipeds and cetaceans were more robust than they are in extant species. Flexibility of the axial skeleton in transitional

mammals also suggests the capability for undulatory propulsion when submerged. Thus, *Ambulocetus* probably resembled a swimming otter in water and a shuffling sea lion on land (Fordyce & Barnes 1994; Thewissen *et al.* 1994). Likewise, the skeletons of *Potamotherium* (Repenning 1976) and *Enaliarctos mealsi* (Berta *et al.* 1989) indicate both otter-like and seal-like locomotor patterns for archaic pinnipeds.

Despite revelations about locomotor mechanisms, the fossil record has provided little insight into the coincident physiological constraints and challenges that accompanied the transitions in morphology and lifestyle. Differences in the mechanics of running and swimming as well as in the thermal properties of air and water would demand different energetic inputs as mammals evolved into aquatic forms. Here, I examine the energetic consequences of such transitions by comparing maintenance and locomotor costs, and the total cost of transport of extant mammals varying in degree of aquatic specialization. Extant terrestrial, semi-aquatic and marine mammals were considered representative of principal evolutionary hallmarks within marine mammal lineages. A comparison of transport costs for these transitional and specialized groups of mammals provided an opportunity to assess the energetic consequences of evolving aquatic locomotion from terrestrial building blocks. The results from this study indicate that running and swimming specialists have converged on an energetic

Table 1. *Energetic costs and swimming speeds of mammalian swimmers*

(Oxygen consumption was determined for animals resting water prior to exercise and during steady-state swimming. Measurements on active animals were done as the subjects swam against a water current in a flume or unrestrained in open water. Oxygen consumption ($mlO_2 kg^{-1} min^{-1}$) was converted to metabolic energy (Joules, J) assuming a caloric equivalent of 4.8 kcal per litre of O_2 and a conversion factor of 4.187×10^3 J $kcal^{-1}$. Minimum COT_{TOT} was determined from the lowest oxygen consumption during swimming divided by speed. Criteria for data selection from the literature included: (i) use of respirometry methodologies for measuring metabolic rates of resting and active animals; (ii) steady-state metabolic levels during measurements; and (iii) non-diving conditions.)

species	mass (kg)	$\dot{V}O_{2rest}$ ($mlO_2 kg^{-1} min^{-1}$)	$\dot{V}O_{2swim}$ ($mlO_2 kg^{-1} min^{-1}$)	COT_{TOT} (J $kg^{-1} m^{-1}$)	speed (m s^{-1})	method
semi-aquatic						
muskrat[b]	0.6	14.7	48.0	21.4	0.75	flume
North American mink[c]	1	20.0	97.5	41.1	0.75	flume
sea otter[d] (surface)	20	13.5	29.6	12.6	0.8	flume
(submerged)	20	13.5	17.6	7.4	0.8[a]	flume
human[e] (elite front crawl	80	24.9	30.0	10.5	1.0	flume
(elite breast stroke)	80	24.9	53.1	16.8	1.0	flume
Marine						
California sea lion[f,g,h]	21	—	13.7	2.3	2.0	flume
	23	6.3	22.0	2.8	2.6	flume
	23	6.6	13.0	2.4	1.8	flume
harbour seal[f,i]	32	—	23.6	3.6	2.2	flume
	33	5.1	15.2	3.6	1.4[a]	flume
	63	4.6	9.6	2.3	1.4[a]	flume
grey seal[j]	104	7.7	15.0	3.9	1.3[a]	flume
bottlenose dolphin[g,k]	145	4.6	8.1	1.3	2.1	ocean swim
killer whale[l]	2738	—	—	0.84	3.1	field respiratory
	5153	—	—	0.75	3.1	rates
grey whale[m]	15000	—	—	0.4	2.1	field respiratory rates

[a] Represents maximum flume speed. Minimum cost of transport speeds based on routine speed of free ranging animals is 1.0 ms^{-1} for submerged sea otters and *ca.* 2.0 ms^{-1} for phocid seals.
[b] Fish 1982.
[c] Williams 1983.
[d] Williams 1989.
[e] Holmer 1972.

[f] Williams *et al.* 1991.
[g] Present study.
[h] Feldkamp 1987.
[i] Davis *et al.* 1985.
[j] Fedak 1986.
[k] Williams *et al.* 1993.
[l] Kriete 1995.
[m] Sumich 1983.

optimum during locomotion that may represent an evolutionary limit for mammals.

2. ASSESSING ENERGETIC COSTS IN SWIMMING MAMMALS

(a) *Metabolism during rest and activity in water*

Metabolic rates have been determined for a variety of swimming mammals that differ markedly in propulsive style. The range of subjects include marine mammals specialized for aquatic locomotion and semi-aquatic mammals that routinely move both on land and in water (table 1). Maintenance costs (MC) of aquatic mammals are assessed from the rate of oxygen consumption ($\dot{V}O_2$) measured on quiescent animals floating quietly under metabolic hoods or breathing into gas-collection bags. To avoid elevations in metabolism associated with thermoregulation, water temperatures in the metabolic chambers are maintained at routine pool, pen, or ocean temperatures for individual animals (i.e. 12–25 °C for the subjects in table 1). Likewise, metabolic depression coincident with diving responses can be a complicating factor. When resting, semi-aquatic mammals such as minks (Williams 1983), muskrats (Fish 1982) and humans (Holmer 1972) remain on the water

surface whereas marine mammals such as seals (Davis *et al.* 1985; Fedak 1986; Williams *et al.* 1991), sea lions (Feldkamp 1987; Williams *et al.* 1991) and dolphins (T. M. Williams, unpublished data) alternate between floating and briefly submerging. The pinnipeds and cetaceans used in the present study submerged for only brief intervals (less than one minute). Therefore, none were considered to be in a diving state. Under these conditions MC includes the energy expended for basal functions as well as endothermy in the alert animal.

Except for cetaceans, the metabolic rates of swimming mammals are often determined on animals trained to swim against a current in a water flume (table 1). Flume dimensions must take into account the frontal area and propulsive movements of each species. In addition, water flows must provide a physiological challenge for the swimmer (Williams 1987). Most of the energetic data for swimming semi-aquatic mammals and smaller marine mammals have been obtained by using open-flow respirometry in conjunction with these flumes. Because most flumes are too small or too slow for studying cetaceans, exercise tests for swimming dolphins, killer whales and grey whales have used several novel approaches. These include measuring physiological parameters while trained

bottlenose dolphins follow a moving boat at sea (Williams *et al.* 1993), and calculating metabolic costs from respiratory patterns of free-ranging killer whales (Kriete 1995) and grey whales (Sumich 1983). A critical feature of these methods is the ability to monitor the subjects at preferred steady state velocities as determined from the routine movements of wild animals.

When comparing the energetics of aquatic mammals it is important to distinguish between swimming and diving activities. In the context of this study, swimming refers to transit swimming in which the course of movement is generally in the horizontal direction and the animal has constant access to air. This differs from diving in which the subject undergoes an extended period of apnea and may initiate a suite of physiological changes including bradycardia, peripheral vasoconstriction and metabolic suppression associated with the dive response (Kooyman 1989). The synergistic metabolic effects of diving superimposed on swimming exercise are beyond the scope of the present study. Therefore, transport costs are compared for transit swimmers only.

(b) *Cost of transport and locomotor costs*

Schmidt-Nielsen (1972) defined the energy cost of locomotion as the amount of fuel it takes to transport one unit of body weight over a unit distance. In the literature, 'total mass specific metabolic rate of the exercising animal divided by speed', as well as, '(total mass specific metabolic rate of the exercising animal minus resting mass specific metabolic rate) divided by speed', have been used interchangeably to define the 'cost of transport'. The former describes the energy required by the individual animal to satisfy both maintenance and locomotor demands during exercise while the latter describes the amount of energy required for moving the body and limbs. These are often termed the total cost of transport (COT_{TOT}) and net cost of transport (COT_{NET}), respectively (Schmidt-Nielsen 1972).

Here, I present total cost of transport (COT_{TOT}), maintenance costs (MC), and locomotor costs (LC) for terrestrial, semi-aquatic and marine species, where

$$COT_{TOT} = MC + LC.$$

COT_{TOT} is calculated by dividing the total metabolic rate of the active animal by locomotor speed. For aquatic mammals, COT_{TOT} represents the energy expended for transit swimming to distinguish it from diving. The difference between COT_{TOT} and MC has been termed the locomotor cost, LC (Williams 1989). This value represents the energy expended by animals for swimming performance and is analogous to COT_{NET} presented for running mammals (Schmidt-Nielsen 1972). To provide a common basis for comparing COT_{TOT} between animals of different size or form of locomotion (Taylor *et al.* 1970), minimum COT_{TOT} for each species is presented (Williams 1987). Energetic costs for mammals are then compared with those of flying birds (Tucker 1973), and salmonid (Brett 1964) and thunniform (Dewar & Graham 1994) fishes.
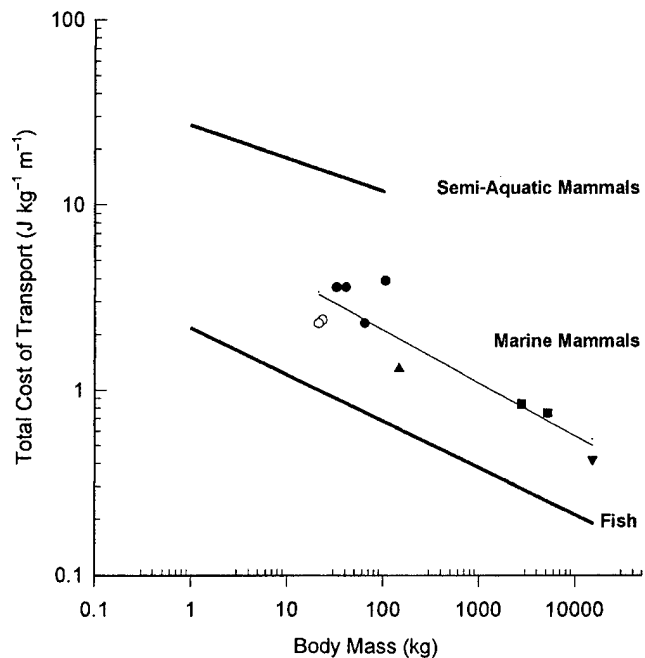

Figure 1. Total cost of transport (COT_{TOT}) in relation to body mass for different classes of swimmers. Individual marine mammals are compared with regressions for semi-aquatic mammals and salmonid fish. Marine mammals include phocid seals (filled circles), California sea lions (empty circles), bottlenose dolphins (upward-pointing triangle), killer whales (squares), and grey whales (downward-pointing triangle) from table 1. The line through the data points is the least squares regression for marine mammals. The lower solid line represents the extrapolated regression for salmonid fish where $y = 2.15x^{-0.25}$ (Brett 1964). The upper solid line shows the regression for swimming semi-aquatic mammals from Williams (1989) where $y = 26.81x^{-0.18}$ and includes data for North American mink, muskrats, humans and surface-swimming sea otters.

3. DISCUSSION

(a) *Energetic costs incurred by swimmers*

The total cost of transport (COT_{TOT}) for swimming mammals may be separated into two distinct groups distinguished by the degree of locomotor specialization (table 1, figure 1). As might be expected, a transitional lifestyle requiring movement between two media sacrifices energetic efficiency for versatility. Thus, semi-aquatic mammals such as minks and muskrats incur transport costs that are 2.4–5.1 times higher than observed for marine mammals (figure 1). Several factors, including hydrodynamic drag (Williams 1989) and propulsive efficiency (Fish 1993, 1996) undoubtedly contribute to the relatively high swimming costs of semi-aquatic mammals. In particular, elevated body drag associated with a surface-swimming position has a profound effect on transport costs. Theoretically, total drag is 4–5 times higher for a body moving on or near the water surface than for the same body submerged (Hertel 1966). This has been demonstrated for humans and harbour seals (Williams & Kooyman 1985), and sea otters (Williams 1989) by towing subjects on the water surface or submerged. Cardiovascular, respiratory and metabolic responses of swimming seals and sea lions also correspond to the percentage of time that the animal

spends on the water surface or submerged while swimming (Williams *et al.* 1991). Similarly, the resulting transport costs for surface and submerged swimming sea otters reflect the differences in body position and drag (table 1).

The total cost of transport is comparatively low in mammals with increased specialization for one form of locomotion. Total transport costs in relation to body mass for swimming marine mammals ranging in size from 21 kg to 15 000 kg is described by

$$COT_{TOT} = 7.79\,mass^{-0.29}\,(r^2 = 0.83, n = 10),$$

where the total cost of transport is in $J\,kg^{-1}\,m^{-1}$ and body mass is in kilograms. This relation expands the observations of Culik & Wilson (1994) and includes otariid and phocid seals, large and small odontocetes, and a mysticete whale (see figure 1). Swimming style in these animals ranges from dorso–ventral undulation in cetaceans (Fish & Hui 1991) to fore-flipper propulsion in otariids (Feldkamp 1987) and lateral undulation of paired hind flippers in phocid seals (Fish *et al.* 1988). In view of the diversity of propulsive styles, it appears that swimming mode has little effect on COT_{TOT} among marine mammals. Similar patterns have been reported for other locomotor groups. For example, transport costs do not vary greatly with the style of swimming in fish (Schmidt-Nielsen 1972, 1984; Bennett 1985), or with bipedal or quadrupedal performance in runners (Taylor & Rowntree 1973; Fedak & Seeherman 1979). Among semi-aquatic mammals, a single allometric expression also describes rowers, paddlers and humans performing the front crawl and breaststroke (Williams 1989).

Despite specialization for aquatic locomotion, the COT_{TOT} of marine mammals are considerably higher than predicted for fish of comparable size (figure 1). Values for pinnipeds including otariids and phocid seals are 2.3–4.0 times those predicted for fish. The COT_{TOT} of cetaceans ranges from 2.1–2.9 times the predicted values. Bottlenose dolphins show the lowest ratio between measured and predicted values within this range (Williams *et al.* 1993). Larger cetaceans such as the killer whale (Kriete 1995) and grey whale (Sumich 1983) demonstrate COT_{TOT} that are 2.2–2.9 times those predicted for salmonid fish.

MC, which reflect inherent differences in endothermy between mammals and fish, appear to account for the discrepancy in COT_{TOT} between these vertebrate groups (figure 2). Endogenous heat production results in a characteristic metabolic disparity between ectotherms and endotherms (Bartholomew 1977). Furthermore, MC for many species of aquatic mammals are exceptionally high owing to the high thermal conductivity of water (Irving 1973; Whittow 1987). Thus, the metabolic rates of many species of aquatic mammal resting in water are 1.7–2.4 times higher than those predicted from allometric regressions for terrestrial mammals resting in air (Kleiber 1975; Williams 1998).

By subtracting the energetic burden of endothermy, we can compare the locomotor costs of marine mammals and fish. In other words, we can compare the amount of energy these animals dedicate to moving their body and appendages through water. This is accomplished by subtracting the MC determined for animals resting in
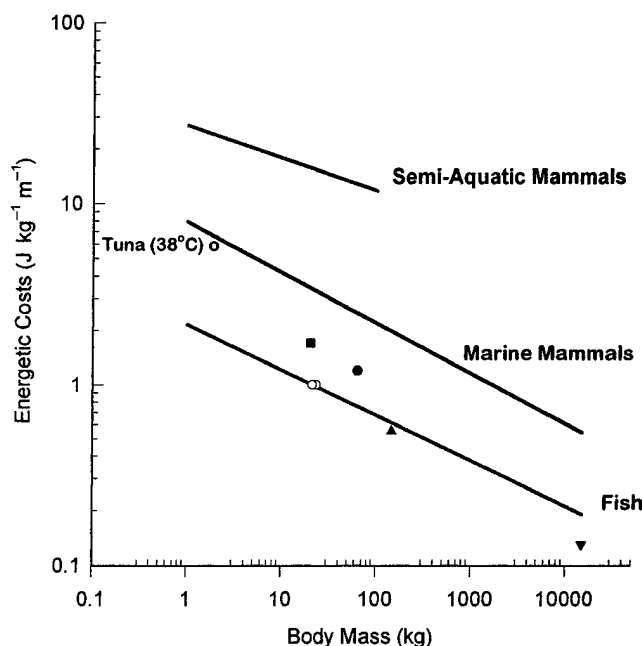

Figure 2. Locomotor costs of marine mammals compared with COT_{TOT} of different classes of swimmers. Solid lines are the allometric regressions for COT_{TOT} of semi-aquatic mammals, salmonid fish and marine mammals as in figure 1. Data points represent the mean locomotor costs (LC) for different species of marine mammal including sea otters (square), California sea lions (plain circle), harbour seals (filled circle), bottlenose dolphins (upward-pointing triangle) and grey whales (downward-pointing triangle). Data are from sources cited in figure 1. The calculated COT_{TOT} for swimming tuna (bold circle) at 38 °C (Dewar & Graham 1994; Dewar *et al.* 1994) is provided for comparison.

water from its corresponding COT_{TOT}. The resulting LC for many species of pinniped and cetacean resemble those predicted from the allometric relation for salmonid fish (figure 2). Values for sea lions and dolphins are within 11% of predictions; even the sea otter, when swimming submerged, shows LC approaching the expected value for fishes. Adult harbour seals are somewhat higher at 58% over predicted while grey whales are lower by 32%.

The energetic costs of endothermic fish also support these findings. Countercurrent heat exchangers allow many species of tuna to conserve metabolic heat and achieve periods of endothermy (Dewar & Graham 1994). Consequences of this thermal specialization (and associated physiological and biochemical modifications) are higher maintenance and transport costs in comparison with ectothermic species. Thus, the COT_{TOT} for yellowfin tuna (*Thunnus albacares*, mean fork length = 51 cm) swimming at 25 °C is 2.75 $J\,kg^{-1}\,m^{-1}$; a value that is 56% higher than predicted for salmonids swimming at the same temperature (Dewar & Graham 1994). By using a Q_{10} of 1.67 determined for yellowfin tuna (Dewar & Graham 1994), we can calculate the theoretical COT_{TOT} for tuna swimming at a mammalian temperature of 38 °C. The resulting value is within 7% of the predicted COT_{TOT} for a similarly sized marine mammal (see figure 2). Although it is unlikely that a tuna would experience such an increase in core temperature (Dewar *et al.* 1994), these calculations serve to illustrate the pathways for evolutionary convergence associated with endothermy and cost efficient

locomotion in large aquatic animals. Both mammals and fish are capable of locomotor thermogenesis, but it appears that the ability to retain endogenous heat dictates the difference in transport costs between these groups.

(b) *Comparisons with other mammalian athletes*

The disparate physical demands for moving on land, through water or through air result in perceptible differences in effort. Among elite animal athletes, evolution and training promote specialized body morphologies and locomotor mechanisms for each form of locomotion. Energetic transport costs usually reflect these specializations and the underlying physical demands of swimming, running and flying (Schmidt-Nielsen 1972; figure 3*a*). An interesting finding in the present study is the nearly identical allometric regressions describing COT_{TOT} for swimming in marine mammals and for running in terrestrial mammals (figure 3*b*). Rather than mode of locomotion, phylogenetic history appears to be an important factor in setting the total energetic cost of active mammals. Total cost of transport for running, swimming and even flying mammals can be described by a single allometric relation

$$COT_{TOT} = 10.02\,\text{mass}^{-0.31}\,(r^2 = 0.92),$$

where COT_{TOT} is cost of transport in $J\,kg^{-1}\,m^{-1}$ and body mass is in kilograms ($n = 55$ individual values representing four species of bat, and 29 terrestrial and six marine mammal species). This relation is indistinguishable from regressions describing transport costs for mammals specialized for running or swimming; bats, however, show COT_{TOT} for flying that are slightly lower than predicted by this regression (figure 3*b*). Neither the slopes nor *y*-intercepts of the allometric regressions for obligate terrestrial or marine mammals are significantly different from the combined regression (table 2). An important factor in these energetic relations is specialization for one mode of locomotion. The allometric regression for semi-aquatic mammals is significantly different from that describing COT_{TOT} for terrestrial mammals (*y*-intercept $t_5 = 4.874$, $p < 0.005$; slope $t_5 = 3.113$, $p < 0.05$). In contrast, comparisons between the regressions for marine and terrestrial mammals demonstrate no significant differences for these locomotor specialists (*y*-intercept $t_8 = 0.558$, $p > 0.25$; slope $t_8 = 0.172$, $p > 0.25$). Thus, we find that the cost of running in a 28 kg goat is identical to the cost of swimming in a 32 kg harbour seal. A 24 kg running dog incurs costs that are only 6% higher. A 107 kg horse maintains a cost of transport within 25% of the cost of swimming for a 104 kg grey seal. COT_{TOT} for a swimming bottlenose dolphin approaches that of a running eland. By comparison, similarly sized semi-aquatic mammals incur costs that are 3–4 times higher.

It is important to recognize that the relative energetic contribution of locomotor and maintenance processes to COT_{TOT} differs for mammals specializing in swimming, flying or running. In general, a greater proportion of the COT_{TOT} is comprised of maintenance costs for many marine mammals in comparison with terrestrial or aerial mammals (figure 4). For example, 22–77% of COT_{TOT} was comprised of maintenance costs in pinnipeds, sea otters, and bottlenose dolphins (table 1). This compares with only 12% in terrestrial mammals and 14% in bats.
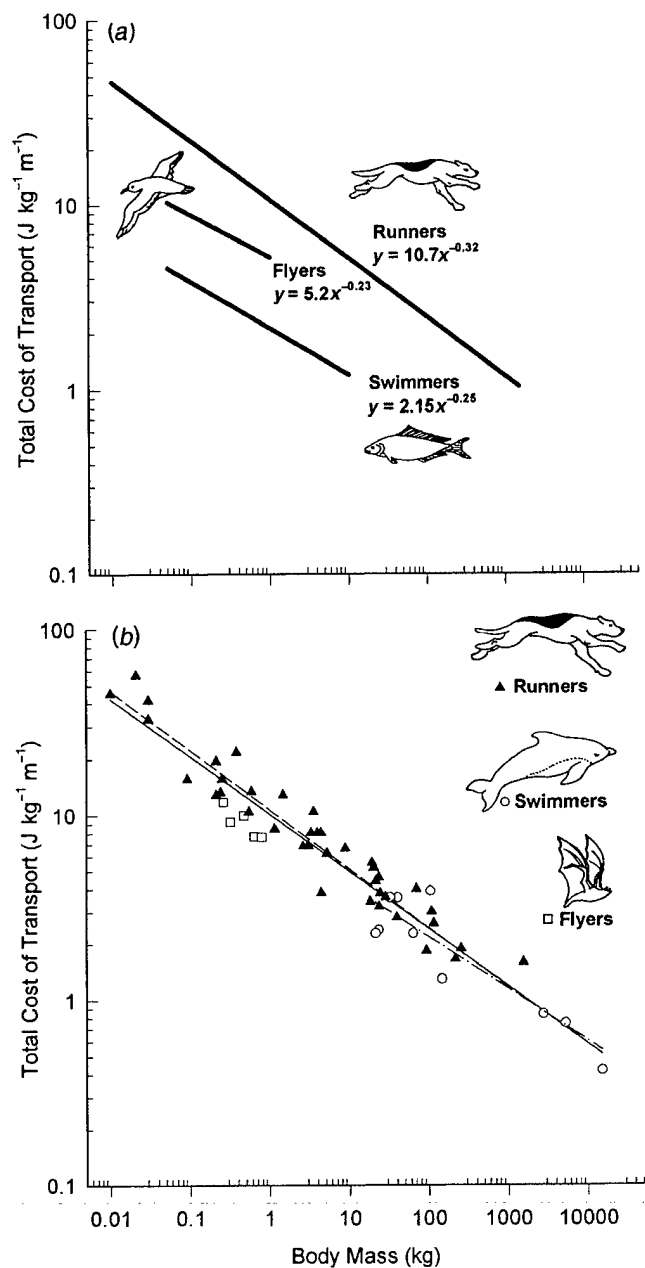

Figure 3. Total cost of transport in relation to body mass for different classes of vertebrates. The conventional comparison for swimming fish, running mammals and flying birds (*a*) is compared with swimming (open circles), flying (open squares) and running (filled triangles) mammals (*b*). (*a*) Regressions are from Tucker (1973) for flyers, Taylor *et al.* (1982) for runners, and Brett (1964) for swimmers, and is based on Schmidt-Nielsen (1972). (*b*) The solid line represents the COT_{TOT} regression for all mammals including flying bats ($n = 5$), swimming marine mammals ($n = 10$) and running terrestrial mammals ($n = 40$). Individual values in (*b*) are from Taylor *et al.* (1982) and Langman *et al.* (1995) for terrestrial mammals, Carpenter (1985, 1986) for bats and as in figure 1 for marine mammals. The dashed and stippled lines show allometric regressions for running and swimming mammals, respectively.

These results support the theoretical predictions of Peters (1983) who suggested that the higher total transport costs of swimming homeotherms in comparison with swimming poikilotherms was owing primarily to proportionately higher maintenance metabolic costs.

Table 2. T-*test statistics comparing the allometric regression describing transport costs for locomoting mammals*

(Costs for all locomoting mammals ($COT_{TOT} = 10.02 \, mass^{-0.31}$, $n = 55$, $r^2 = 0.92$) are compared to the regressions for swimming marine mammals ($COT_{TOT} = 7.79 \, mass^{-0.29}$, $r^2 = 0.83$, $n = 10$) and running terrestrial mammals ($COT_{TOT} = 10.7 \, mass^{-0.32}$ from Taylor *et al.* 1982). Regressions for cost of transport versus body mass (log–log transformed) were determined using least squares methods (Zar 1974). Differences in the slopes and *y*-intercepts of allometric regressions for marine and terrestrial mammals, and for semi-aquatic mammals and locomotor specialists were evaluated. Regression parameters were computed from the sources and data in table 1 for marine and semi-aquatic mammals, and taken from the published literature for running mammals (Taylor *et al.* 1982) including elephants (Langman *et al.* 1995).)

	y-intercept	slope
terrestrial mammals		
t_{38}	1.6	0.5
$p>$	0.05	0.25
marine mammals		
t_8	0.42	0.13
$p>$	0.25	0.25

Figure 4. Percentage of COT_{TOT} attributed to maintenance costs in flying, swimming and running mammals. Height of the bars and vertical lines represent mean percentage of $COT_{TOT} + 1$ s.e. for each group. Maintenance costs were determined from the metabolic rates of animals resting in air or water prior to exercise as described in the text. Data are from sources cited in figure 3. Numbers in parentheses represent number of species.

When LC and MC are taken into account, the results of this study remain consistent with previous studies concerning the relative energetic cost of swimming, flying and running (Schmidt-Nielsen 1972; Tucker 1975). That is, the cost of swimming is lower than that of other forms of locomotion (figure 3a). In mammals specialized only for swimming, LC rather than COT_{TOT} resemble the values predicted for fish (figure 2). The implication is that the energy dedicated to moving the body and limbs varies with locomotor mode and is most economical for swimmers. However, the total energetic cost (COT_{TOT}) incurred by the swimming marine mammal is much higher. It is this total cost that cannot be distinguished from values reported for mammalian runners and flyers (figure 3b). Viewed as the entire energetic demand required for moving from one place to another, COT_{TOT} takes on an ecological relevance. Free-ranging animals must contend with the total energetic expenditure associated with supporting basic biological functions as well as with moving the body and appendages through the environment. COT_{TOT} provides an indication of the sum of these expenses, and perhaps should be termed the excursion cost or ecological cost of transport (Garland 1983) to differentiate it from the standard usage of cost of transport.

(c) *Optimizing oxygen delivery during locomotion*

It is not intuitively obvious why the cost of swimming in fish should be lower than flight in birds and why both of these are energetically cheaper than running. Indeed, the high drag of the aquatic environment would have suggested the opposite. Runners must expend energy to overcome gravity, whereas swimmers overcome hydrodynamic drag, and flyers contend with both aerodynamic drag and gravity (Schmidt-Nielsen 1972). To date, it is unclear which of these, if any, posed the greatest evolutionary challenge to mammalian energetic pathways.
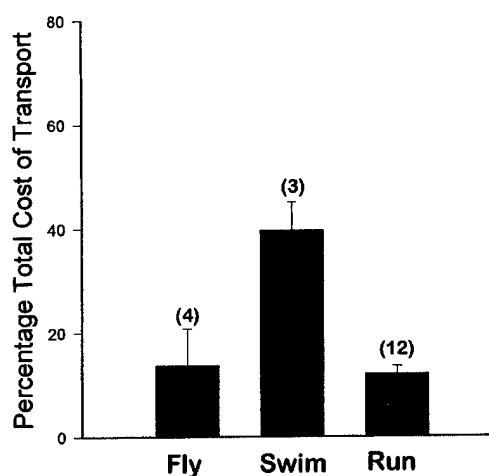
The similarity in total transport costs for terrestrial, aquatic and aerial mammalian specialists (figure 3b) suggests a physiological rather than mechanical limit for COT_{TOT}. Tucker (1975) indicated that the comparatively low mean muscular efficiency of running animals accounted for their higher costs of transport. Similarly, Taylor and colleagues (Taylor *et al.* 1980; Taylor 1987) have proposed that the observed differences in transport costs between swimmers, runners and flyers may result from differences in the cost of generating muscular force rather than in doing work against the environment *per se*. Variations in the energetic cost for size-specific recruitment of individual fibre types in skeletal muscles may also account for differences in transport costs (Rome 1992). A closer examination of the two parameters used to calculate transport costs, locomotor velocity and the rate of oxygen consumption during exercise, provides additional insights regarding the costs for different modes of locomotion. The velocities associated with the minimum COT_{TOT} for different forms of locomotion do not follow the pattern observed for running, swimming and flying costs. Swimming fish and running mammals of comparable body mass tend to move at similar minimum COT_{TOT} speeds, whereas flying birds move considerably faster (Peters 1983). For example, fish ranging from 0.06 kg salmonids (Brett 1964) to 2.2 kg yellowfin tuna (Dewar & Graham 1994) swim at $0.30–1.1 \, m \, s^{-1}$. Similarly sized mammals show minimum cost running speeds ranging from *ca.* $0.2 \, m \, s^{-1}$ to $0.6 \, m \, s^{-1}$ while similarly sized birds fly 15–30 times faster (Tucker 1973). Likewise, flying mammals move at $7–8 \, m \, s^{-1}$ while terrestrial counterparts barely approach $0.6 \, m \, s^{-1}$. The minimum COT_{TOT} speed is *ca.* $2.0 \, m \, s^{-1}$ for many marine mammals regardless of the size of the swimmer (Videler & Nolet 1990; table 1). Yet, a sea otter-sized terrestrial mammal runs at $0.8 \, m \, s^{-1}$ and a dolphin-sized terrestrial mammal shows a minimum COT_{TOT} speed of over $6.5 \, m \, s^{-1}$ (Taylor *et al.* 1982). Based on the relative costs for

swimming, flying and running (figure 3*a*), the order in which we would expect the fastest performances would be: fish, birds, and terrestrial mammals. Instead, flyers routinely outperform both runners and swimmers.

The ability of an animal to take in, deliver and translate oxygen into muscular work during exercise affords a qualitative explanation for the differences in COT_{TOT} for animals. Structural and functional variations along the respiratory system appear to correlate with limits in oxidative metabolism (Weibel *et al.* 1987; Taylor *et al.* 1987*a*). The diffusing capacity of the lungs, cardiac output, and capillary volume and total mitochondrial volume within the locomotor muscles are important factors in setting the aerobic capacity of terrestrial athletes (Taylor *et al.* 1987*b*). Comparable details are not available for the respiratory pathways of other vertebrate groups. However, comparisons of the efficiency of gas-exchange organs have been made for piscine, avian and mammalian systems. These studies indicate that the countercurrent gills of fish are the most efficient vertebrate respiratory system for extracting oxygen from the surrounding medium. This is followed by the cross-current system of birds and finally the open pool system of mammals (Piiper & Scheid 1982; Scheid 1982). Interestingly, the relative differences in COT_{TOT} for swimming fish, flying birds and running mammals (figure 3*a*) parallel the theoretical sequence in gas exchange efficiency among these vertebrate groups.

It is likely that the gas-exchange systems of these groups operate below their theoretical limits under normal physiological conditions (Scheid 1982). Yet, inherent differences in the efficiency of the oxygen pathway, whether at the level of the oxygen uptake, delivery or use by the skeletal muscles, could provide clues about the relation between physiological limits and the optimum energetic costs during locomotion. Mammals tend to preferentially select locomotor speeds that result in the lowest energetic cost (Hoyt & Taylor 1981). If the oxygen pathway operates at near maximum efficiency at these preferred speeds, then the similarity in COT_{TOT} for mammals regardless of whether they are swimming or running (figure 3*b*) is not as surprising.

Clearly, further research regarding the efficiency of the oxygen pathway for different mammalian groups is needed. In addition, it is difficult to predict if the same patterns will apply to other vertebrate groups. Evolutionary pressures as well as the malleability of the oxygen pathway may be very different for birds, lizards and fish, and warrant further investigation.

(d) *The evolution of cost efficient swimming in mammals*

These results permit us to speculate about the energetic challenges faced by ancestral marine mammals. The physiological building blocks available to the first mammalian expatriates into the aquatic environment would have been those of a terrestrial specialist, i.e. a mammal designed primarily for moving on land. Assuming that the same physiological constraints act on extant mammals, the energetic trend during evolution would have been from the low transport costs of the terrestrial specialist to the high costs of amphibious species followed by a return to the initial low cost level in
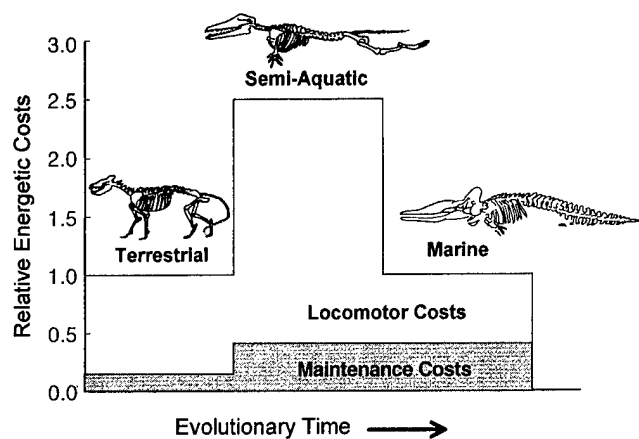

Figure 5. Theoretical changes in COT_{TOT}, locomotor costs and maintenance costs with the evolution of fully marine living mammals. The evolutionary pathway assumes that ancestral marine mammals included an obligate terrestrial form that was followed by a semi-aquatic form (i.e. *Ambulocetus*) and finally an obligate marine form. The solid lines at the top denote relative COT_{TOT}. The white and grey areas designate locomotor and maintenance costs, respectively. Note the similarity in COT_{TOT} for terrestrial and marine specialists despite the change in the relative contribution of locomotor and maintenance costs. (Skeletons redrawn from Berta 1994.)

the aquatic specialist (see figure 5). With increased morphological specialization (Fish 1996), and consequently increased proficiency in the water, energetic costs for locomotion could be reduced. Thus, in evolving an aquatic lifestyle primitive marine mammals probably encountered and overcame an energetic hurdle in terms of transport costs only to return to energetic levels dictated by their terrestrial ancestry. Such an energetic hurdle initially seems counter to the argument that natural selection maximizes fitness along an evolutionary pathway. However, locomotor and physiological mechanisms are only part of the energetic equation for ancestral animals (Alexander 1996). The selective forces for entering the aquatic environment (i.e. favourable climatic conditions, ecological or habitat opportunities, the exploitation of previously untapped food resources; Fordyce 1989; Fordyce & Barnes 1994) undoubtedly provided an energetic benefit to the mammal. Presumably, these benefits surmounted the energetic difficulties associated with entering the water. Furthermore, limiting the duration of initial forays into the water may have reduced energetic disadvantages in the form of high maintenance and locomotor costs. This strategy is observed in extant semi-aquatic mammals such as the North American mink (*Mustela vison*; Williams 1986) and Australian water rat (*Hydromys chryogaster*; Fanning & Dawson 1980). By maintaining a labile core body temperature and limiting aquatic activity to short periods these mammals gain the energetic advantage of additional prey resources while minimizing energetic disadvantages. Consequently, minks and water rats establish an overall balance in costs and benefits by shuttling between energetic peaks and valleys. A similar mechanism in ancestral marine mammals would have relegated the proposed energetic hurdle to a transient phenomenon.

The resulting COT_{TOT} for extant marine mammals are higher than predicted for salmonid fish, but further evolutionary or energetic improvements are unlikely. Without the energetic burden of endothermy many marine mammals show locomotor costs approaching those of fish, a group that has the lowest cost of transport among vertebrates (Schmidt-Nielsen 1972). If, as these results imply, marine mammals have reached an energetic optimum in terms of locomotor costs, then COT_{TOT} may only be reduced by altering the comparatively high maintenance costs (figure 4). This may be accomplished by entering a hypometabolic state, an energy conserving strategy observed for some marine mammals during prolonged apneas associated with diving (Hochachka & Guppy 1987; Hurley 1996). Such a physiological mechanism may also explain the exceptionally low transport costs of submerged-swimming beavers (Allers & Culik 1997) and platypus (Fish *et al.* 1997).

Current evidence suggests that specialists among mammals have converged on an energetic optimum for locomotion. Unexpectedly, the phocid seals, otariids, odontocetes and mysticetes independently evolved into forms with swimming transport costs equivalent to those of running mammals. Regardless of the style of propulsion or locomotor mode (figure 3b), mammals appear to expend similar levels of energy to move a kilometre, albeit at different speeds and maintenance costs. This implies a preferred limit in aerobic efficiency along the pathway for oxygen in mammalian systems. Taylor and colleagues (1987a,b) have suggested that structural and functional limitations along this pathway dictate aerobic performance capacities in terrestrial athletes. The present study indicates that similar limitations may apply to aquatic mammals. To maximize performance within these limitations the energetically efficient swimmer will specialize for one locomotor event, and thus improve chances for successfully hunting prey, escaping predators or winning in Olympic competitions.

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Body size and skeletal muscle myoglobin of cetaceans: adaptations for maximizing dive duration

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Abstract

Cetaceans exhibit an exceptionally wide range of body mass that influence both the capacities for oxygen storage and utilization; the balance of these factors is important for defining dive limits. Furthermore, myoglobin content is a key oxygen store in the muscle as it is many times higher in marine mammals than terrestrial mammals. Yet little consideration has been given to the effects of myoglobin content or body mass on cetacean dive capacity. To determine the importance of myoglobin content and body mass on cetacean diving performance, we measured myoglobin content of the *longissimus dorsi* for ten odontocete (toothed whales) and one mysticete (baleen whales) species ranging in body mass from 70 to 80 000 kg. The results showed that myoglobin content in cetaceans ranged from 1.81 to 5.78 g (100 g wet muscle)$^{-1}$. Myoglobin content and body mass were both positively and significantly correlated to maximum dive duration in odontocetes; this differed from the relationship for mysticetes. Overall, the combined effects of body mass and myoglobin content accounts for 50% of the variation in cetacean diving performance. While independent analysis of the odontocetes showed that body mass and myoglobin content accounts for 83% of the variation in odontocete dive capacity. © 2000 Elsevier Science Inc. All rights reserved.

Keywords: Cetaceans; Myoglobin; Body size; Diving capacity; Odontocetes; Mysticetes

1. Introduction

Cetaceans exhibit a 2200-fold increase in body mass from the smallest species, the 55 kg vaquita (*Phocoena sinus*; Evans, 1987), to the largest species, the 122 000 kg blue whale (*Balaenoptera musculus*; Laurie, 1933). Such a wide range of body masses results in an exceptionally large range of metabolic rates and capacities for oxygen storage in comparison to other marine mammal groups. Although both factors will impact diving

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capability (Kooyman et al., 1981), there is little information concerning the advantages or disadvantages associated with extreme body size and the capacity to adapt the mammalian body for prolonged periods of submergence. One important adaptation for diving exhibited by a wide range of diving mammals is the storage of oxygen in the skeletal muscles (Castellini and Somero, 1981). Myoglobin acts as the primary oxygen carrier in the skeletal muscles of these mammals. When perfusion to a muscle region is decreased, oxygen depletion of that area is retarded by the release of myoglobin-bound oxygen into the tissue (Salathe and Chen, 1993). Elevated myoglobin content in the skeletal muscle enables aerobic

metabolism to be maintained during apnea and appears to be an important adaptation for diving in birds and mammals. Consequently, myoglobin concentration is 10–30 times greater in the locomotor muscles of aquatic birds and mammals than in the muscles of their aerial or terrestrial counterparts (Kooyman, 1989).

For the species studied to date, cetaceans demonstrate a higher reliance on muscle oxygen stores than other marine mammal groups including pinnipeds. For example, ≈ 33, 38, and 51% of the total body oxygen store is found in the skeletal muscle of beluga whales (Shaffer et al., 1997), bottlenose dolphins (Williams et al., 1993) and narwhals (Williams unpublished observation), respectively. In comparison, otariids and phocids sequester a higher proportion of the total oxygen store in the blood; less than 33% of the oxygen reserve of pinnipeds is found in the skeletal muscle (Kooyman, 1989). A non-diving mammal, the human, stores only 15% of its oxygen reserve in the skeletal muscle.

In contrast to numerous investigations on pinniped muscles (Scholander, 1940; Lenfant et al.,

1970; George et al., 1971; Castellini and Somero, 1981; Lydersen et al., 1992; Ponganis et al., 1993; Thorson 1993), comparatively few studies have examined the skeletal muscles of cetaceans or the adaptations of their muscles for diving. One previous study suggested that cetaceans with higher muscle myoglobin contents show longer dive durations (Snyder, 1983). A complicating factor, however, is the effect of body mass on dive performance in this diverse marine mammal group. In view of this, we examined the myoglobin content of the primary locomotor muscles of 11 species of cetaceans, ranging in size from the 70 kg common dolphin to the 80 000 kg bowhead whale. These data were then correlated with reported values for maximum dive duration for each species. We found that both muscle myoglobin content and body mass explained nearly 50% of the variation in dive performance across cetacean species. Differences in foraging behavior between the two cetacean suborders, odontocetes (toothed whales) and mysticetes (baleen whales), suggest that foraging behaviors may further influence these relationships.

2. Materials and methods

2.1. Animals

Muscle samples were obtained from ten odontocete species and one mysticete (Table 1). The cetaceans examined in this study were acquired from strandings, incidental fishery catches, or subsistence hunts. Muscle samples were taken only from mature animals that were considered in excellent condition based on their external appearance (i.e. no bloating or large external cuts). Depending on the availability of specimens, one to seven individuals of each species were analyzed.

2.2. Muscle sample collection

For the bowhead and beluga whales, muscle samples were collected on site soon after death. For all other species, whole carcasses were frozen at 0°C shortly after death and muscle samples were taken within 6 months postmortem. All muscle samples were stored at − 80°C until analysis. Muscle samples were taken from the midbelly of the longissimus dorsi (Fig. 1). The longissimus dorsi is the primary locomotor muscle of

Table 1
Myoglobin contents for the longissimus dorsi of the cetacean species examined in this study[a]

Cetacean species	n	[Mb] (g [100 g wet muscle]$^{-1}$)
Odontocetes		
Common dolphin (*Delphinus capensis*)	3	3.58 ± 0.32
Common dolphin (*Delphinus delphis*)	7	3.55 ± 0.27
Harbor porpoise (*Phocoena phocoena*)	2	4.03 ± 0.32
Striped dolphin (*Stenella coeruleoabla*)	1	5.78
Northern right whale dolphin (*Lissodelphis borealis*)	1	1.81
Pacific white-sided dolphin (*Lagenorhynchus obliquidens*)	2	3.45 ± 0.25
Bottlenose dolphin (*Tursiops truncatus*)	6	2.66 ± 0.16
Pygmy sperm whale (*Kogia breviceps*)	1	4.33
Beluga whale (*Delphinapterus leucas*)	5	3.44 ± 0.39
Cuvier's beaked whale (*Ziphius cavirostris*)	2	4.32 ± 0.15
Mysticetes		
Bowhead whale (*Balaena mysticetus*)	5	3.54 ± 0.33

[a] All values are for site 1 illustrated in Fig. 1. *n*, represents the number of specimens for each species. Values are given as the mean ± 1 S.E.M.
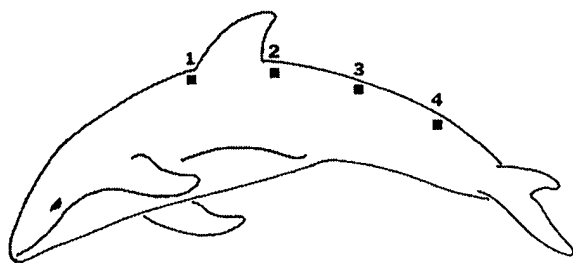
Fig. 1. Sample sites for skeletal muscle in cetaceans. Numbered black squares indicate the four areas along the *longissimus dorsi* where the muscle samples were taken. All muscles were sampled from the midbelly region at each site. Samples (≈ 6 g) were obtained from site 1 for all of the specimens in this study.

cetaceans and is one of two muscles that power the dolphin upstroke (Pabst, 1993). Recent research suggests that there is a gradient in myoglobin content between the midbelly and the peripheral regions of the *longissimus dorsi* of cetaceans (Harrison and Davis, 1998). The midbelly appears to contain the highest concentration of myoglobin. In addition, a small gradient in myoglobin content is found along the length of the muscle, with the area below the dorsal fin showing the highest content (Harrison and Davis, 1998). Sample site 1 in the present study (Fig. 1) was chosen to reflect the highest myoglobin content for the *longissimus dorsi* of each species. When available, samples were also taken from three other sites along the muscle (sites 2, 3, and 4; Fig. 1) for comparative purposes.

2.3. Myoglobin content

Myoglobin content ([Mb]), measured in g Mb (100 g wet muscle)$^{-1}$ was determined using the procedure of Reynafarje (1963). Slightly thawed muscle samples (≈ 0.5 grams) were minced in a low ionic strength buffer (40 mM phosphate, pH = 6.6), and sonicated (Sonifier Cell Disrupter Model W185D, Heat systems-Ultrasonics, Inc.) for 2–3 min on ice. The buffer to tissue ratio was 19.25 ml buffer per g wet tissue. The samples were centrifuged at $-4°C$ and 28 000 g for 50 min (Sorvall RC-5B refrigerated superspeed centrifuge, DuPont Instruments). The clear supernatant was drawn, and bubbled at room temperature with pure CO for approximately 8 min. We added 0.02 g of sodium dithionite to ensure a complete reduction. The absorbance of

each sample was read at room temperature at 538 and 568 nm on a spectrophotometer (Shimadzu UV-visible spectrophotometer Bio spec-1601). All samples were run in triplicate.

2.4. Standards for the assays

Myoglobin contents were determined for the main locomotory skeletal muscles of a New Zealand white rabbit and a 7 day old Northern elephant seal pup, and compared to previously published values. The [Mb] of the seal pup in the present study, 2.4 $\pm$ 0.2 g (100 g wet muscle)$^{-1}$, was similar to a previously published value for a 1–14 day old northern elephant seal pup (Thorson, 1993). The [Mb] for rabbit muscle, 0.08 $\pm$ 0.06 g (100 g wet muscle)$^{-1}$, was similar to previous reports for a New Zealand white rabbit (Castellini and Somero, 1981).

2.5. Dive duration

Maximum dive times for each species were obtained from previous studies that used time-depth recorders (TDRs) or trained animals. Timed observations of dive durations for wild, uninstrumented animals were included only if no other data source was available. *Kogia breviceps* was not used in the diving analyses because the only dive data available for this species was acquired from a rehabilitated animal that had been housed in a shallow pool for several months before release (Hohn et al., 1995). We used maximum dive durations rather than average dive times in these analyses for several reasons. First, few diving records for cetaceans report average dive durations; of the 15 species used in our analyses, only six have average dive times reported in the literature. Second, average values are a poor indicator of an animal's diving capabilities. This is illustrated by comparing average and maximum dive durations of the six cetacean species for which both values are available. Average dive duration is 1.1 min for the harbor porpoise (Westgate et al., 1995), 0.4 min for the Pacific white-sided dolphin (Black, 1994), 0.4 min for the bottlenose dolphin (Mate et al., 1995), 12.9 min for the beluga whale (Martin et al., 1993), 38 min for the sperm whale (Watkins et al., 1993), and 6.3 min for the bowhead whale (Wursig et al., 1984). These values represent less than 20% of the maximal dive durations reported for these species. The

beluga and sperm whales are exceptions; their average dive durations are 70 and 52% of their maximum dive durations, respectively. Similar to studies examining aerobic function in terrestrial mammals (Weibel et al., 1987), we have chosen to use extreme performance in this study to understand the physiological capacities of diving in cetaceans.

2.6. Statistics

Variability between the myoglobin contents of skeletal muscle sites, and between species was determined by Kruskal–Wallis one way analysis of variance on ranks. In addition, Dunn's method for all pairwise comparison procedures was used for interspecies comparisons. Species specific muscle myoglobin contents determined in the present study were combined with previously published values for other cetacean species for further analyses. The inclusion of previously reported values ensured that the myoglobin-dive duration relationships determined in this study were inclusive of as many cetacean species possible. The same species were subsequently used in body mass-dive duration relationships. Least squares methods were used for the linear regressions of myoglobin content versus maximum dive duration, and for body mass in relation to maximum dive duration. The regressions for body mass were plotted on logarithmic scales due to the large range in body mass (70–80 000 kg). The reported linear equation for this plot was log transformed. Significance of the regressions was determined using an F-test. A Pearson correlation test was used to determine the correlation between body mass and muscle myoglobin. The simultaneous effects of body mass and muscle myoglobin content on maximum dive performance were assessed using a forward stepwise regression. Results were considered significant when $P \leq 0.05$. All statistical tests were calculated using standard software programs (Sigma Stat, Jandel Scientific, 1995).

3. Results

3.1. Myoglobin content

Myoglobin contents for each of the four sampling sites and the average value for the four sites were not significantly different in 10 specimens of *Lagenorhynchus obliquidens*, *Delphinus delphis* and *Delphinus capensis* ($H = 1.11$, df = 4, $P = 0.89$). Therefore, values for site 1 (Fig. 1) are used as a representative of the entire muscle; these are reported as mean values ± 1 S.E.M.

Myoglobin contents for the *longissimus dorsi* of cetaceans measured in this study are presented in Table 1. There was a 3-fold increase in myoglobin content from the lowest value in the Northern right whale dolphin, 1.81 g (100 g wet muscle)$^{-1}$, to the highest value in the striped dolphin, 5.78g (100 g wet muscle)$^{-1}$. The one mysticete examined in this study, the bowhead whale, had a myoglobin content of 3.54 g (100 g wet muscle)$^{-1}$; that was within the mid-range of values for the odontocetes. The interspecific differences in myoglobin contents were significant ($H = 18.37$, df = 10, $P = 0.049$, $n = 11$) although an all pairwise test was unable to identify the particular species that were different.

For review, previously published myoglobin contents for the skeletal muscles of cetaceans are presented in Table 2. The combined myoglobin data for all cetacean species, including previously reported values and data from the present study, show that the range of myoglobin values for the mysticetes (0.91–3.54 g [100 g wet muscle^{-1}]) are at the lower range of myoglobin values for the odontocetes (1.81 to 7.87 g [100 g wet muscle^{-1}]) (Tables 1 and 2).

3.2. Myoglobin content and body mass relationships with dive capacity

The results of the literature search for the accumulation of the body mass and dive capacity data for the cetacean species used in the analyses for this study are presented in Table 3.

Myoglobin content of the skeletal muscle correlated poorly with maximum dive duration for all cetaceans ($r^2 = 0.28$, $F = 5.03$, $P = 0.04$, $n = 15$). When the two cetacean suborders were analyzed independently, we found that the correlation increases for odontocetes while the relationship for mysticetes was not significant (Fig. 2). For odontocetes, maximum dive duration increased with myoglobin content according to the relationship:

Odontocete maximum dive duration

$$= 8.31 \text{ Mb} - 13.10 \ (r^2 = 0.36, \ F = 5.69, \ P$$

$$= 0.04, \ n = 12)$$

Table 2
Previously reported myoglobin contents for cetacean skeletal muscle

Cetacean species	[Mb] (g [100 g wet muscle]$^{-1}$)	References
Odontocetes		
Indus river dolphin (*Platanista indi*)	2.6	(Blessing, 1972)
Spotted dolphin (*Stenella attenuata*)	2.54	(Castellini and Somero, 1981)
Spinner dolphin (*Stenella longirostris*)	5.5	(Dolar et al., 1999)
Fraser's dolphin (*Lagenodelphis hosei*)	7.1	(Dolar et al., 1999)
Humpback dolphin (*Sousa chinensis*)	2.5	(Harrison and Davis, 1998)
Narwhal (*Monodon monoceros*)	7.87	(Williams unpubl. observ.)
False killer whale (*Pseudorca crassidens*)	6.3	(Harrison and Davis, 1998)
Northern bottlenose whale (*Hyperoodon ampullatus*)	6.34	(Scholander, 1940)
Sperm whale (*Physeter macrocephalus*)	5.03	Avg. of Scholander (1940) and Tawara (1950)
Mysticetes		
Sei whale (*Balaenoptera borealis*)	0.91	(Tawara, 1950)
Fin whale (*Balaenoptera physalus*)	2.42	Avg. of Scholander (1940) and Hochachka and Foreman (1993)

Table 3
Body mass and maximum dive durations for cetaceans[a]

Cetacean species	Mass[d] (kg)	Max. dive (min)	Method[b]	References[c]
Odontocetes				
Common dolphin (*Delphinus capensis*)	70[e]	5	TDR	(Heyning and Perrin, 1994; Evans, 1971)
Common dolphin (*Delphinus delphis*)	70[e]	5	TDR	(Heyning and Perrin, 1994; Evans, 1971)
Harbor porpoise (*Phocoena phocoena*)	70[h]	5.35	TDR	(Westgate et al., 1995)
Spotted dolphin (*Stenella attenuata*)	75[e]	4.7	TDR	(Perrin et al., 1987; Scott et al., 1993)
Northern right whale dolphin (*Lissodelphis borealis*)	115[e]	6.25	O	(Jefferson et al., 1993; Leatherwood and Walker, 1979)
Pacific white-sided dolphin (*Lagenorhynchus obliquidens*)	120	6.2	E	(Whole body specimen mass from present study; Black, 1994)
Bottlenose dolphin (*Tursiops truncatus*)	200[e]	8	E	(Evans, 1987; Ridgway and Harrison, 1986)
Pygmy sperm whale (*Kogia breviceps*)	363[e]	12	TDR	(Evans, 1987; Hohn et al., 1995)
Beluga whale (*Delphinapterus leucas*)	1400[f]	18.3	TDR	(Bryden, 1972; Martin et al., 1993)
Narwhal (*Monodon monoceros*)	1500[h]	25	TDR	(Heide-Jφrgensen and Dietz, 1995)
Cuvier's beaked whale (*Ziphius cavirostris*)	2953[f]	30	O	(Bryden, 1972; Houston, 1991)
Northern bottlenose whale (*Hyperoodon ampullatus*)	6700[e]	60	O	(Evans, 1987; Reeves et al., 1993)
Sperm whale (*Physeter macrocephalus*)	36,700[g]	73	TDR	(Omura, 1950; Watkins et al., 1993)
Mysticetes				
Sei whale (*Balaenoptera borealis*)	23,000[g]	20	O	(Lockyer and Waters, 1986 Martin, 1990)
Fin whale (*Balaenoptera physalus*)	33,000[g]	14	TDR	(Lockyer and Waters, 1986; Watkins et al., 1981)
Bowhead whale (*Balaena mysticetus*)	80,000[e]	31	TDR	(Evans, 1987; Wursig et al., 1984)

[a] Species: listed are limited to those with known myoglobin contents and dive behaviors.
[b] Dive data acquired by: TDR, time depth recorder; E, experimental dive; or O, observation.
[c] References: body mass reference first, followed by dive duration reference.
[d] Mass given, unless otherwise noted in table, is represented as.
[e] Average mass for the species.
[f] Calculated mass from body length-mass equations.
[g] Mass corrected by 6% for loss associated with piecemeal weighing.
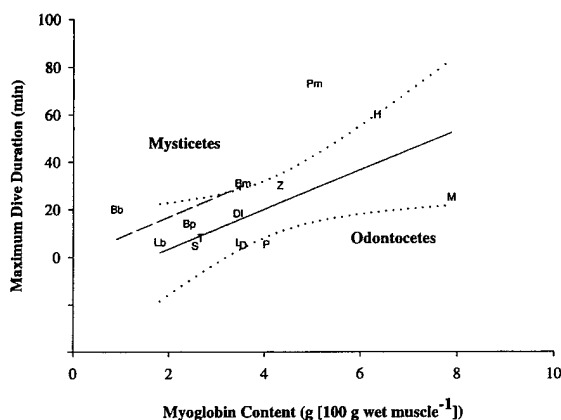[h] Estimated mass of animal from which dive data was acquired.

Fig. 2. Maximum dive duration in relation to skeletal muscle myoglobin content for odontocetes (solid line) and mysticetes (dashed line). Relationships are least squares linear regressions as described in the text. Dotted lines are the 95% confidence intervals around the regression for odontocetes. Genus initials denote data points; species initial is included if the genus initial is redundant. See Table 1, Table 2, and Table 3 for references. (Odontocetes: S, *Stenella attenuata*; D, *Delphinus delphis* and *Delphinus capensis*; P, *Phocoena phocoena*; L, *Lagenorhynchus obliquidens*; Lb, *Lissodelphis borealis*; T, *Tursiops truncatus*; Dl, *Delphinapterus leucas*; M, *Monodon monoceros*; Z, *Ziphius cavirostris*; H, *Hyperoodon ampullatus*; Pm, *Physeter macrocephalus*; Mysticetes: Bb, *Balaenoptera borealis*; Bp, *Balaenoptera physalus*; Bm, *Balaena mysticetus*).
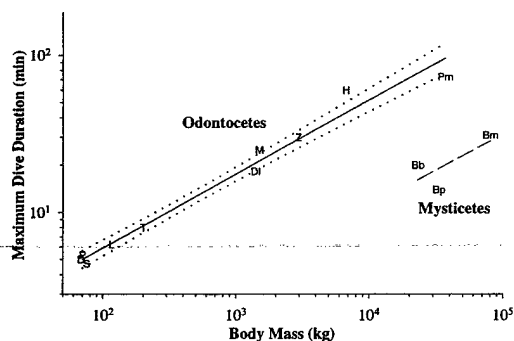

Fig. 3. Maximum dive duration in relation to body mass for odontocetes (solid line) and mysticetes (dashed line). Relationships are least squares linear regressions as described in the text. Dotted lines are the 95% confidence intervals around the regression for odontocetes. Genus initials denote data points; species initial is included if the genus initial is redundant. See Table 3 for references. (Odontocetes: S, *Stenella attenuata*; D, *Delphinus delphis* and *Delphinus capensis*; P, *Phocoena phocoena*; L, *Lagenorhynchus obliquidens* and *Lissodelphis borealis*; T, *Tursiops truncatus*; Dl, *Delphinapterus leucas*; M, *Monodon monoceros*; Z, *Ziphius cavirostris*; H, *Hyperoodon ampullatus*; Pm, *Physeter macrocephalus*; Mysticetes: Bb, *Balaenoptera borealis*; Bp, *Balaenoptera physalus*; Bm, *Balaena mysticetus*).

where duration is in min and muscle myoglobin is in g Mb (100 g wet muscle)$^{-1}$. For mysticetes, the relationship between myoglobin content and maximum dive duration was not significant ($r^2 = 0.33$, $F = 0.48$, $P = 0.61$, $n = 3$).

Similar results were found for the body mass and dive capacity analyses. A significant correlation was found between maximum dive duration and body mass for all cetaceans in this study ($r^2 = 0.72$, $F = 33.49$, $P < 0.001$, $n = 15$). Again the relationships differed between the two cetacean suborders. Odontocetes exhibit a significant correlation between maximum dive duration and body mass (Fig. 3) according to the relationship:

Odontocete max. dive duration

$$= 0.68 \ (\text{body mass})^{0.47}$$

($r^2 = 0.98$, $F = 463.92$, $P < 0.001$, $n = 12$)

where duration is in min and body mass is in kg. The same relationship was not significant for mysticetes ($r^2 = 0.54$, $F = 1.15$, $P = 0.48$, $n = 3$) (Fig. 3).

Pearson correlation tests showed that cetacean muscle myoglobin content and body mass, and odontocete muscle myoglobin content and body mass are not correlated ($r = -0.08$, $P = 0.77$, $n = 15$ and $r = 0.49$, $P = 0.16$, $n = 10$, respectively). Because these two variables are independent, we ran forward stepwise regression analyses to determine the combined influence of these two characteristics (muscle myoglobin content and body mass) on maximum dive duration. For all cetaceans combined, muscle myoglobin and body mass together explained 50% of the variation in maximum dive duration across species (myoglobin $r^2 = 0.28$, $P = 0.017$; body mass delta $r^2 = 0.22$, $P = 0.042$). For odontocete species only, body mass and muscle myoglobin together explained 83% of the variation in maximum dive duration across odontocete species (body mass $r^2 = 0.69$, $P < 0.001$; myoglobin delta $r^2 = 0.14$, $P = 0.023$). A similar test for the mysticete species was not possible due to the small sample size available for analyses.

4. Discussion

Limits to aerobic diving are determined by the size of the oxygen store as well as the rate in which this store is utilized. Because skeletal mus-

cles provide the power for swimming, an important factor in determining maximum dive duration of marine mammals is size of the on-board oxygen stores to support metabolic processes at the level of the working skeletal muscle (Hochachka, 1986). Previous studies have demonstrated that aerobic metabolic processes within the muscle may be maintained during prolonged periods of submergence by utilization of oxygen stored in myoglobin (Kooyman, 1989). From the present study it appears that the combined effect
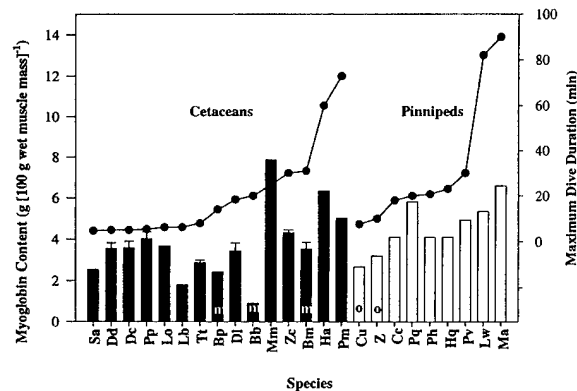

Fig. 4. Muscle myoglobin content (bars) and maximum dive duration (-●-) for cetaceans (black bars) and pinnipeds (white bars). Individual species are presented in order of increasing dive duration. 'm' denotes mysticetes and 'o' denotes otariids. Initials denote genus and species. Note that our calculations show that in pinnipeds, myoglobin concentration correlates with maximum dive duration according to the relationship, dive duration = 18.7 [Mb] − 51.4 ($r^2 = 0.58$, $F = 9.82$, $P = 0.017$, $n = 9$). The relationship between maximum dive duration and myoglobin content is more variable in cetaceans as described in the text. See Table 1, Table 2, and Table 3 for cetacean references. (Sa, *Stenella attenuata*; Dd, *Delphinus delphis*; Dc, *Delphinus capensis*; Pp, *Phocoena phocoena*; Lo, *Lagenorhynchus obliquidens*; Lb, *Lissodelphis borealis*; Tt, *Tursiops truncatus*; Bp, *Balaenoptera physalus*; Dl, *Delphinapterus leucas*; Bb, *Balaenoptera borealis*; Mm, *Monodon monoceros*; Zc, *Ziphius cavirostris*; Bm, *Balaena mysticetus*; Ha, *Hyperoodon ampullatus*; Pm, *Physeter macrocephalus*). Pinniped references Otariids: Cu, *Callorhinus ursinus*: [Mb] (Lenfant et al., 1970; Castellini and Somero, 1981), Dive (Gentry et al., 1986); Z, *Zalophus californianus*: [Mb] (Castellini and Somero, 1981), Dive (Feldkamp et al., 1989). Phocids: Cc, *Cystophora cristata*: [Mb] and Dive (Scholander, 1940); Pg, *Phoca groenlandica*: [Mb] and Dive (George et al., 1971); Ph, *Phoca hispida*: [Mb] (Lydersen et al., 1992), Dive (Parsons, 1977); Hg, *Halichoerus grypus*: [Mb] (Scholander, 1940), Dive (Lavigne and Kovacs, 1988); Pv, *Phoca vitulina*: [Mb] (Lenfant et al., 1970; Castellini and Somero, 1981), Dive (Kooyman et al., 1972); Lw, *Leptonychotes weddelli*: [Mb] (Ponganis et al., 1993), Dive (Castellini et al., 1993); Ma, *Mirounga angustirostris*: [Mb] (Thorson, 1993), Dive (Le Boeuf et al., 1993).

of muscle myoglobin content as well as body mass dictates the limits to diving performance in cetaceans. As discussed below, feeding behaviors unique to odontocetes and to mysticetes may have refined these relationships over evolutionary time.

By itself, myoglobin content of the skeletal muscle is a poor predictor of maximum dive duration when cetaceans are considered as a single group (Fig. 4). However, when the two cetacean suborders are analyzed independently, we find a close correlation between myoglobin content and maximum dive duration, particularly for the odontocetes (Fig. 2). Thus, the four odontocete species exhibiting the longest maximum dive durations (25–73 min) have high myoglobin contents ranging from 4.32 to 7.87 g (100 g wet muscle)$^{-1}$. In comparison, short duration divers among the odontocetes with maximum dive durations of 5 to 18.3 min maintain comparatively lower myoglobin contents (1.81 to 4.03 g [100 g wet muscle]$^{-1}$). These results suggest that high myoglobin content within the skeletal muscles serves as an important adaptation for prolonging dive duration in odontocetes. Indeed, some of the longest dives for cetaceans occur among the odontocetes, including the narwhal, Cuvier's beaked whale, Northern bottlenose whale, and sperm whale (Table 3).

In contrast to the results for odontocetes, the relationship between myoglobin content and maximum dive duration for mysticetes was not significantly correlated (Fig. 2). This may be due in part to the low sample size available for analysis for the mysticetes (Tables 1 and 2). These results differ from Snyder (1983) who suggested that large cetaceans have elevated myoglobin contents that correspond to increased dive duration. The results also differ from the pattern reported for pinnipeds, a mammalian group that demonstrates a distinct positive correlation between myoglobin content and maximum dive time (Fig. 4). Furthermore, pinnipeds may be subdivided into two groups, shorter diving otariids that maintain low myoglobin contents and longer diving phocids with higher myoglobin contents. The current study did not find a similar distinction between the two groups of cetaceans, the mysticetes and odontocetes (Fig. 4).

The wide range of body masses among cetacean species has a demonstrable effect on the range of maximum dive durations reported for these mammals (Table 3). Although body mass was posi-

tively correlated with maximum dive duration for cetaceans, the effect of body mass differs between the two cetacean suborders. A strong correlation between body mass and maximum dive duration was found for odontocetes; the same relationship was not significant for mysticetes (Fig. 3). Again, this may have been related to the small sample size of mysticetes examined. To maintain equivalent sample sizes for the myoglobin-dive duration and body mass-dive duration analyses, we limited our analyses to those species in which myoglobin content was measured or known. Although it was difficult to draw conclusions in the present study, previous investigations have reported a positive correlation between body mass and dive duration for mysticetes (Schreer and Kovacs, 1997).

For Weddell seals (Kooyman et al., 1983), other pinnipeds (Costa, 1991), and the pekin duck (Hudson and Jones, 1986) large body size provides an advantage for diving in terms of the absolute size of oxygen stores and relative decrease in mass specific metabolic rate. Similarly, both muscle myoglobin content and body mass influence dive capacity in cetaceans. These two characteristics explain nearly 50% of the variation in dive performance across a wide range of cetacean species including odontocetes and mysticetes. When odontocetes are considered separately, muscle myoglobin content and body mass accounts for 83% of the variation in dive performance.

Increased body size preadapts large cetaceans for prolonged dive durations due to two factors; (1) an increase in the absolute muscle mass and consequently an increase in absolute muscle oxygen stores; and (2) a decrease in mass specific metabolic rate. Metabolic rate only increases by a mass exponent 0.75 for resting mammals (assuming cetaceans follow the same allometric trend presented for other animals by Kleiber 1975) and by 0.71 for swimming transport costs in marine mammals (Williams, 1999). The lower mass specific energetic demands of large cetaceans in comparison to smaller cetaceans slow the relative depletion of oxygen during breath-hold. Thus, the larger cetacean is able to prolong its dive time beyond that of smaller cetaceans despite similar mass specific muscle oxygen stores. A comparison of the 80 000 kg bowhead whale and the 70 kg common dolphin demonstrates these relationships. These species represent two size extremes among cetaceans that have similar myoglobin

contents in the locomotor muscles (Table 1). Based on the Kleiber (1975) regression, the mass specific metabolic rate of the common dolphin is 10 times greater than that of the bowhead whale. The theoretical consequence is a lower oxygen utilization rate for the larger cetacean, and sparing of limited oxygen stores in the skeletal muscle. With similar myoglobin contents per gram of muscle, the difference in oxygen utilization rate permits longer dive durations in the larger cetacean. TDR records support this, and we find a 6-fold greater maximum dive duration for the bowhead whale in comparison to the common dolphin (Table 3). Admittedly, further research is required to provide empirical evidence regarding the scaling of oxygen demand in this taxonomic group. However, these simple calculations demonstrate the importance of body size on metabolic rate and its potential effect on diving performance.

Despite the small sample sizes for mysticetes in this study, it appears that the relationships between myoglobin content and maximum dive duration (Fig. 2) and body mass and maximum dive duration (Fig. 3) are different for the two cetacean sub groups. One possible explanation for this is differences in preferred feeding behaviors and consequently different selective pressures for prolonged diving in odontocetes and mysticetes. The largest species in this study, the bowhead whale, dives between 0.1–31 min with an average dive duration of 12.08 ± 9.15 min (Wursig et al., 1984). These whales are described as skimmer feeders and forage primarily at the water surface, exhibiting a stereotypic basic pattern of short dive durations (Wursig et al., 1984; Dorsey et al., 1989). Other mysticete species show similar surface foraging behaviors. For example, in the Gulf of California and coastal California the majority of dives by fin whales rarely exceed 12 min and 200 m in depth (Croll personal communication). This depth represents only 12 times the animals' body length and suggests that large mysticetes may rarely approach their physiological limits for diving. In view of this, many species of mysticetes may be under little selective pressure for developing physiological adaptations, such as high myoglobin contents, that prolong dive duration. Conversely, the sperm whale, the largest odontocete, forages at depths of up to 2250 m (Ridgway and Harrison, 1986) for durations of 73 min (Watkins et al., 1993). When feeding behavior is

taken into account, it is not surprising that large odontocetes show exceptionally high myoglobin contents in the skeletal muscles while large mysticetes do not (Figs. 2 and 4, Tables 1 and 2).

In summary, the results of the present study demonstrate how myoglobin concentration in the skeletal muscles and body mass mutually influence dive duration in cetaceans. These two characteristics combined account for nearly 50% of the variation in dive capacity across cetacean species that vary in body mass from 70 to 80 000 kg. As found for other marine mammals, enhanced oxygen storage capacity due to high myoglobin concentrations is an important adaptation for diving in cetaceans. Balancing this store and oxygen utilization rate will dictate the duration of aerobically supported dives for these animals (Kooyman, 1989). Due to the wide range of body masses among cetaceans, differences in oxygen utilization rate as modulated by mass specific metabolic rate, is an especially important factor in defining aerobic dive capacity. Differences observed between the two cetacean suborders suggest that odontocetes and mysticetes have been under different selective pressures for developing physiological adaptations for prolonged dive duration. Among cetaceans, mysticetes show average myoglobin contents and rely on the relatively low oxygen consumption rates associated with large body size to support relatively short dives. The trend for smaller odontocetes is elevated muscle myoglobin contents prolonging dive durations. Large odontocete species, such as the bottlenose whale and sperm whale, combine both large body mass and high myoglobin contents in the skeletal muscles. As a result, these cetaceans are capable of prolonged dives at remarkable depths making them the champion divers among cetaceans.

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THE DIVING PHYSIOLOGY OF BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*)

II. BIOMECHANICS AND CHANGES IN BUOYANCY AT DEPTH

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Summary

During diving, marine mammals must balance the conservation of limited oxygen reserves with the metabolic costs of swimming exercise. As a result, energetically efficient modes of locomotion provide an advantage during periods of submergence and will presumably increase in importance as the animals perform progressively longer dives. To determine the effect of a limited oxygen supply on locomotor performance, we compared the kinematics and behavior of swimming and diving bottlenose dolphins. Adult bottlenose dolphins (*Tursiops truncatus*) were trained to swim horizontally near the water surface or submerged at 5 m and to dive to depths ranging from 12 to 112 m. Swimming kinematics (preferred swimming mode, stroke frequency and duration of glides) were monitored using submersible video cameras (Sony Hi-8) held by SCUBA divers or attached to a pack on the dorsal fin of the animal. Drag and buoyant forces were calculated from patterns of deceleration for horizontally swimming and vertically

diving animals. The results showed that dolphins used a variety of swimming gaits that correlated with acceleration. The percentage of time spent gliding during the descent phase of dives increased with depth. Glide distances ranged from 7.1±1.9 m for 16 m dives to 43.6±7.0 m (means ± S.E.M.) for 100 m dives. These gliding patterns were attributed to changes in buoyancy associated with lung compression at depth. By incorporating prolonged glide periods, the bottlenose dolphin realized a theoretical 10–21 % energetic savings in the cost of a 100 m dive in comparison with dives based on neutral buoyancy models. Thus, modifying locomotor patterns to account for physical changes with depth appears to be one mechanism that enables diving mammals with limited oxygen stores to extend the duration of a dive.

Key words: dolphin, *Tursiops truncatus*, diving, biomechanics, buoyancy.

Introduction

Animals demonstrate a wide variety of mechanical, morphological and behavioral adaptations that promote locomotor efficiency and subsequently reduce the overall cost of activity. Terrestrial animals systematically change gaits, moving from walk to trot to gallop as speed increases (Heglund et al., 1974; Taylor, 1978; Hoyt and Taylor, 1981; Magana et al., 1997). During walking, these animals conserve energy by alternately storing and releasing gravitational potential energy as they rotate over a stiffened limb. With the change to a gallop, bound or hop, elastic elements in the limbs and spine may be used to store and recover energy as the speed of a terrestrial animal increases (Taylor, 1978; Williams, 1983).

Similarly, aquatic vertebrates use a variety of strategies to reduce the cost of locomotion. Burst-and-glide swimming and schooling, observed in many species of fish, promote energy conservation (Fish et al., 1991). The low drag associated with

gliding periods during interrupted forms of swimming appears to compensate for the increased effort of re-acceleration during burst phases (Blake, 1983). Schooling behavior also reduces the energetic cost for individuals moving in groups by decreasing the relative drag encountered by the trailing swimmers (Breder, 1965; Belyayev and Zuyev, 1969; Weihs, 1973; Abrahams and Colgan, 1985).

Locomotor efficiency is especially important for aquatic mammals during diving. When submerged, marine mammals must balance the energetic demands of exercise with the conservation of a limited oxygen store (Castellini, 1985; Castellini et al., 1985). High locomotor costs will presumably lead to the termination of a dive as oxygen reserves are quickly depleted. Conversely, locomotor efficiency may be manifest as an increase in time available at depth for locating and catching prey or for predator avoidance (Williams, 1996).

Most studies addressing locomotor performance in marine

mammals have focused on transit-swimming animals moving near the water surface (Fish, 1992). For example, the routine speeds (Lang and Norris, 1966; Lang, 1974; Würsig and Würsig, 1979; Williams et al., 1992), boundary flow characteristics (Rohr et al., 1998) and burst performances (Hui, 1987) of bottlenose dolphins have been reported. In comparison, there is little information concerning the underwater performance capabilities and limitations of these animals. In view of this, the present study examined the behavior and biomechanics of diving bottlenose dolphins (*Tursiops truncatus*) and the effect of a limited oxygen supply on underwater performance. Factors contributing to locomotor efficiency during submergence were investigated. To assess the relationships between swimming mode, stroke mechanics and dive depth, we videotaped dolphins during (1) horizontal swimming near the water surface, (2) horizontal swimming at depth, and (3) vertical diving to depths ranging from 12 to 112 m. Digital analyses of the video sequences were used to define locomotor modes and their pattern of use, glide duration and rates of acceleration and deceleration. These data, in combination with information from time/depth and velocity recorders, allowed changes in drag and buoyancy due to depth to be determined. The results of this study indicate that dolphins exploit changes in buoyancy associated with pressure changes at depth. By incorporating prolonged glide periods during descent, dolphins can reduce the period of active stroking and related energetic costs. Thus, glide performance by dolphins provides one important mechanism for conserving limited oxygen stores during submergence.

Materials and methods

Animals

Six trained Atlantic bottlenose dolphins (*Tursiops truncatus*) were used in this study (Table 1). All animals were housed in net pens (>15 m×15 m×4 m deep) connected to the open ocean. The dolphins were fed a diet of capelin and herring supplemented with multivitamins (Sea Tabs™, vitamin C, B-12 and B complex). Five of the animals were housed at the Dolphin Experience (Grand Bahama Island, Bahamas). Two adult male dolphins (B1, B2) and one adult female (B3) were used during uninstrumented dives to 12–14 m and for horizontal swims on the water surface and while submerged. A second female (B4) and an immature male (B5) were also used for surface swimming tests. Deep dives and horizontal submerged swims were performed by an adult male dolphin (S6) wearing an instrument package. This animal was housed at the U.S. Navy SPAWAR Systems Center (San Diego, California, USA).

Experimental design

The swimming mechanics and behavior of dolphins were examined under four conditions: (1) steady-state horizontal swimming near the water surface, (2) horizontal swimming at depths of 5–14 m, (3) shallow dives to 12 m without instrumentation on the dolphins, and (4) deep dives ranging

Table 1. *Age and morphological dimensions of the bottlenose dolphins used in this study*

Animal	Age (years)	Length (cm)	Fluke span (cm)	Mass (kg)	Location
B1	13	249	64	236	Bahamas
B2	13	254	72	227	Bahamas
B3	13	237	68	173	Bahamas
B4	13	233	61	177	Bahamas
B5	2	188	N/A	82	Bahamas
S6	16	236	66	177	San Diego

Age was estimated from body length and duration in captivity.

Body length is the straight-line distance from the tip of the rostrum to the fluke notch.

N/A, not applicable.

from 16 to 112 m with the animal wearing an instrumentation package. Horizontal swimming, both near the surface and at depth, was used to evaluate the swimming mode of dolphins in the absence of changes in buoyancy. Deep dives of 16–112 m allowed a comparison of locomotor behaviors as buoyancy and demands on oxygen reserves changed with the depth and duration of the dive. Swimming and gliding performance of dolphins with and without instrumentation were also compared to determine the potential effects of the instrument package on the locomotor behavior and hydrodynamic drag of the animals.

Horizontal swimming

The kinematics of bottlenose dolphins swimming near the water surface was recorded using a hand-held video camera (Sony Hi-8, model CCD TR400). Dolphins were videotaped while swimming alongside a 17 foot Boston Whaler traveling at either 1.5 or 3.7 m s^{-1}. Boat speed was controlled by maintaining the outboard motor at constant revs min^{-1} with the same motor trim for all runs. Speed associated with each revs min^{-1} was determined by videotaping the boat's passage past fixed points a measured distance apart. Video sequences of the fixed points were digitized, and speed was determined using a motion-analysis system (Peak Performance Technologies, Inc.; Englewood, CO, USA). Trainers maintained the position of the dolphins abeam of the boat outside the stern and bow wakes. Analyses were limited to video segments in which the dolphins remained clear of interfering wakes and were stationary relative to the moving boat.

Horizontal swimming was also examined for submerged dolphins moving between two trainers at a depth of 14 m or between stationary targets at approximately 5 m depth. During the 14 m trials, movements of the dolphins were recorded by a SCUBA diver with a hand-held video camera in a submersible housing (Stingray, Inc.). The camera was held in a stationary position perpendicular to the swimming path of the animals. Progress across the field of view was converted to speed (m s^{-1}) using the motion-analysis system described above.

Images were digitized and calibrated against the measured length of the dolphin. To account for extraneous movements of the camera, a fixed point on the sea floor within the field of view was digitized using Peak Performance software (Englewood, CO, USA). Movement vectors of the fixed point were then subtracted from movement vectors of the dolphin. In addition to these trials, fluke movements of a dolphin swimming horizontally at approximately 5 m depth were recorded for an animal wearing a submersible video/instrument package (described below). Horizontal swim paths at depth ranged from 10 to 100 m in length.

Shallow dives

Straight-line dives to less than 16 m in depth were recorded in the Bahamas by a SCUBA diver using a hand-held video camera in a submersible housing (described above). On each experimental day, two dolphins followed a motor boat to an open ocean site 1 mile (1.61 km) offshore. Sites ranged from 12 to 16 m in depth with a sand bottom. Dolphins were trained to dive between the boat and a trainer stationed at depth. The animals chose their rates of ascent and descent, surface interval between dives and bottom time. Each session was recorded by a diver positioned perpendicular to the movements of the dolphins and as far back as visibility allowed. Depending on the distance from the subject, the field of view for the camera was 7–14 m. A field of view of 14 m allowed the entire ascent and descent of the dolphins to be monitored without panning the camera. When necessitated by surge, a monopod was used to stabilize the camera. To control for inadvertent camera movement, a stationary reference point was digitized, and its movement vector was subtracted from the dolphin's track. Measurements of fluke movement and velocities were not sensitive to camera range because each video sequence was calibrated against the measured length of the dolphin.

Deep dives

Fluke movements during deep (16–112 m) diving were recorded by a submersible video camera worn by the dolphin. A saddle platform containing the camera and instrumentation was custom-fitted to the dorsal fin of one dolphin, S6. The dolphin was trained for 6 weeks prior to the experiments to swim and dive while wearing the instrument package. This on-board system enabled us to examine the fluke movements of the dolphins at depths exceeding 100 m, which were outside the range of SCUBA divers.

The instrument package included a time/depth recorder, velocity meter, camera head (See-snake) surrounded by blue light-emitting diodes and video recorder. The camera head was directed backwards to record the stroke activity of the dolphin's fluke. Video sequences and dive variables were synchronized using custom-designed software (Pisces Design; San Diego, CA, USA). The instrument package and platform were neutrally buoyant and constructed of non-compressible materials to maintain neutrality at depth. The mass of the package was 14 kg, representing 8 % of the dolphin's mass. Because the package was neutrally buoyant, there was no

additional weight for the dolphin to bear. However, its mass affected the acceleration of the dolphin. Details of the camera and instrument package are described by Davis et al. (1999).

The stall speed and accuracy of the velocity meter, as well as the accuracy of the time/depth recorder, were determined prior to deployment. The minimum recording (stall) speed of the velocity meter was measured by towing the instrument package attached to a fusiform shape through an annular water trough (Scripps Institute of Oceanography, La Jolla, CA, USA). In addition, the velocity meter was self-calibrated on the diving dolphin by plotting the velocity of the animal against the rate of depth change (S. Blackwell, personal communication). The latter method provides accurate calibration of the velocity meter if any portion of a dive is near vertical. Observations from the surface and video recordings indicate that this condition was met in the present study. The depth sensor was calibrated before and after the experimental period. The accuracy of the depth sensor was tested on a pressure station at 0–1500 psi (0–10.4 MPa) and was found to be linear over the test range (r^2=0.99) with a mean standard deviation of ±0.2 %. Depth and velocity were recorded at 1 s intervals throughout the dives.

Ten dives to 16 m were conducted inside San Diego Bay, CA, USA. During these trials, the dolphin followed a boat (Boston Whaler, 21 foot) to the dive site, where the instrument package was placed on the dolphin and secured using a strap. An acoustic pinger attached to a video camera was lowered to 16 m. The camera was cabled to a monitor on the boat and used to confirm the animal's arrival at depth. Following a signal from the trainer, the dolphin submerged to the pinger. On arrival, the acoustic signal was turned off and the animal returned immediately to the boat. A rest period of at least 1 min was provided between dives. The mean rest period was 46±23 s before the dolphin voluntarily began diving.

Eighteen dives of 50–112 m were conducted in the open ocean approximately 5 miles (8.1 km) off the coast of San Diego, CA, USA. To avoid fatigue during these deep diving tests, the dolphin was transported by boat to the dive site, where it was immediately returned to the water. The instrument package was placed on the dolphin, and the acoustic pinger was lowered to the test depth (50 or 100 m). Testing procedures were as described for 16 m dives. Recovery periods averaged 2.5 min between dives, during which the respiratory rate of the animal was monitored. Respiratory rate was determined by counting the number of breaths taken during the first minute immediately following the dive (Williams et al., 1999).

Analysis

The swimming mode and kinematics of uninstrumented dolphins were determined from video sequences from the hand-held camera using a motion-analysis system (Peak Performance Technologies, Inc.; Englewood, CO, USA). Each swimming or diving segment was converted to digital format. Anatomical points of interest (for details, see Fig. 1A) were manually digitized for 1–60 images per second of video recording. The acceleration, deceleration, angular acceleration

and speed of each point were then computed. In addition, stroke amplitude and the distance traveled by the dolphins while stroking or gliding were assessed for each video sequence. Changes in the amplitude (as a proportion of total body length) of the anatomical points were calibrated against the measured length of each dolphin.

Video images from the instrument package worn by the dolphin on deep dives were copied onto VHS tapes with data overlay from the time/depth recorder and velocity meter. The annotated video recording was analyzed 'frame by frame' for patterns in swimming mode and type of stroke. Strokes were categorized as large, medium, small or gliding according to the arc swept by the fluke. Stroke type was correlated to changes in depth, speed and acceleration of the dolphin.

Drag and buoyant forces were determined from videotaped sequences of horizontally swimming or vertically diving dolphins, respectively. Total body drag was calculated by multiplying the measured rate of deceleration of horizontally gliding dolphins by the total mass decelerated. Deceleration was determined from the change in speed at 1 s intervals and averaged over the glide period. The mass of dolphin S6 was 177 kg, and the mass of the instrument package was 14 kg. Because accelerating a body within a fluid also involves accelerating the surrounding fluid (Daniel, 1984; Lovvorn et al., 1991; Vogel, 1981), we accounted for the mass of the entrained water moving with the dolphin. This is equivalent to the mass of water displaced by the animal multiplied by the coefficient of added mass (0.06 for a prolate spheroid of fineness ratio 5.0; Vogel, 1981). On the basis of this calculation, the mass of the entrained water was 11 kg, and the total mass of the instrumented animal moving through the water was 202 kg. It is likely that the coefficient of added mass used in these calculations is conservative for a dolphin-shaped body and that the actual added mass may be greater because of water entrained by body contours or fins. Calculations based on a less-streamlined shape (i.e. a fineness ratio of 4.0) result in only a 2.1 % increase in the predicted total mass of the instrumented animal. Such a difference would not significantly alter our calculations for body drag and buoyant force.

Buoyancy in diving dolphins was calculated from the differences in deceleration between vertical and horizontal glides. The changes in buoyancy were ascribed to changes in volume with depth due to the compression of air spaces by water pressure. For dolphins, the lungs represent an important, compressible air space. Air in the lungs imparts a buoyant force equal to the amount of water displaced according to Archimedes' principle (Giancoli, 1984). During diving, pressure increases by 1 atm (98.1 kPa) for every 10 m increase in depth (Heine, 1995). Because volume varies inversely with pressure, the lung volume of the dolphins will decrease with depth. On the basis of these principles, the change in air volume of the lungs is described by:

$$V_D = V_S/(1 + 0.1h), \qquad (1)$$

where V_D is air volume in liters at depth, V_S is the air volume

in liters at the surface, and h is depth in meters. The buoyant force at any depth can be determined for the dolphin from lung volume added to the buoyant force of its body. The resulting equation is:

$$B_D = V_D g + B_B, \qquad (2)$$

where B_D is the buoyant force in newtons at depth, V_D is the air volume in liters at depth from equation 1, g represents the acceleration due to gravity (9.8 m s^{-2}) and B_B is buoyancy in newtons of the dolphin's body without air (−33.2 N for dolphin S6; see equation 7). Note that the air volume in liters is equivalent to the mass of the displaced water in kilograms. During vertical glide sequences, upward buoyant forces oppose the downward pull of gravity. The resultant force will hereafter be referred to as a positive buoyant force when the net force is upwards and as a negative buoyant force when the net force is downwards.

Effects of instrumentation on dolphin performance

Previous studies indicate that the addition of recording instruments may alter the performance of an aquatic animal by increasing drag and by adding inertial mass (Wilson et al., 1986; Boyd et al., 1997). The total frontal area of the instrument package in the present study represented approximately 22 % of the dolphin's frontal area. The instruments were evenly divided between each side of the dolphin, with the front end of the instruments being tapered to minimize drag. We determined the changes in total body drag of the dolphins due to the instrument package by comparing horizontal glide deceleration for instrumented and uninstrumented animals. Behavioral and mechanical effects of instrument drag were also assessed by comparing the stroke type, stroke frequency and speed of instrumented and uninstrumented dolphins. Data for uninstrumented dolphins were obtained from digital analysis of video recordings taken by a SCUBA diver. For the instrumented dolphin, data were obtained from video recordings as well as from velocity and depth recorders in the instrument package.

Statistics

Linear and curvilinear regressions were determined from least-squares methods using Sigma Plot (Jandel Scientific, 1995). Sigma Stat software (Jandel Scientific, 1995) and Zar (1974) were used for t-tests of paired data. Sums-of-squares analyses for curves were calculated using SuperAnova software. Values for significance were set at $P<0.05$. Means are reported ±1 S.E.M.

Results
Swimming gaits of bottlenose dolphins

Similar to previous reports (Videler and Kamermans, 1985; Fish and Hui, 1991), we found that the entire body of the dolphin oscillates as it swims. An undulatory wave progresses behind the dorsal fin down the peduncle to the fluke hinge and finally to the fluke tip (Fig. 1). The dorsal fin moves out of phase with the rostrum and fluke. Maximum upward excursion
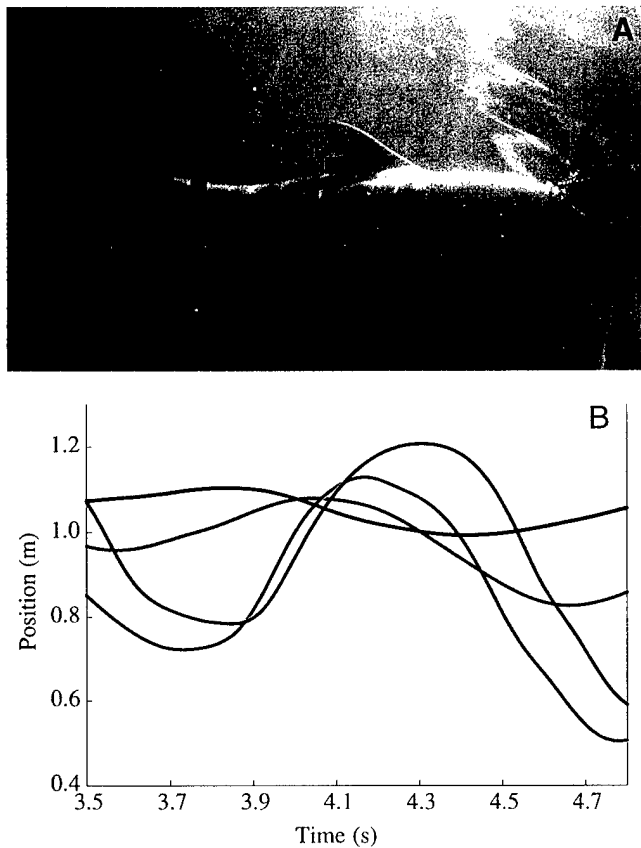
Fig. 1. Video image (A) and range of movement (B) of four anatomical sites during a single stroke for a bottlenose dolphin swimming horizontally next to a boat at 1.5 m s^{-1}. Colored squares in the picture correspond to the line colors illustrating the movements for each site. Note that the dorsal fin (dark blue) reaches its maximum excursion first, followed sequentially by the peduncle (red), the fluke hinge (green) and finally the fluke tip (pink).

frequency of these movements were dependent on the speed and power requirements of the animal (Table 2). Both the present study and that of Fish (1993) found no change in fluke amplitude during steady swimming over the range of test speeds. Three different patterns or gaits were observed.

Large-amplitude strokes

The largest stroke amplitudes (representing 20–50 % of body length) occurred at the start of horizontal swims and at the beginning of the descent and ascent phases of dives. The amplitude of these strokes exceeded the range reported for steadily swimming dolphins in an aquarium pool at speeds ranging from 1.2 to 6.0 m s^{-1} (Fish, 1993). The use of this gait corresponded to the periods of greatest acceleration (3.5–4.7 m s^{-2}). The amplitudes for all body segments were larger than those observed during steady swimming. The greatest change in amplitude occurred at the rostrum and was four times that of steady swimming. In comparison, the fluke and dorsal fin regions more than doubled their amplitude during periods of acceleration, while the mid-peduncle region showed the least change (Table 2).

As a result of the methodology, only the movements of the flukes could be recorded during deep dives or horizontal swims at depths exceeding 14 m. Large-amplitude strokes were used during the initial 1–2 s of horizontal swims and initial descents of dives. The period for large-amplitude stroking increased up to 5 s during the initial ascent from 50 and 100 m dives.

Medium-amplitude strokes

Medium-amplitude strokes (approximately 20 % of body length) occurred during steady-state swimming at 1.5–3.7 m s^{-1}. Motion of the head was reduced in comparison with that occurring in association with large-amplitude strokes. The arc of the rostrum covered only 5 % of body length during medium-amplitude stroking. Similarly, the dorsal fin showed comparatively smaller amplitude movements.

There was a significant (P=0.05) increase in the frequency of medium-amplitude strokes with speed during steady swimming over the range 0.6–3.7 m s^{-1} (Fig. 2A). Dolphins

of the fluke tip occurs as the dorsal fin is at the bottom of its cycle; the reverse occurs on the downstroke. Each anatomical site differed in range of movement. The amplitude and

Table 2. *Primary locomotor modes of swimming and diving bottlenose dolphins*

Gait	Use	Duration	Stroke frequency (Hz)	Amplitude (% body length) R:D:F
Large-amplitude	Acceleration	Brief (1–5 s)	>0.43×speed (1.5 to >3 Hz)	20:10:40 Declines rapidly as speed increases
Medium-amplitude	Cruising	Extended (1 s to >1 min)	0.43×speed (0.5–3 Hz)	5:5:20
Glide	Energy conservation	Dependent on dive depth (1–50 s)	0	0:0:0

Stroke frequency increased linearly with speed during steady swimming (see text). During periods of acceleration, stroke frequency was higher than indicated by this relationship.

Relative changes in stroke amplitudes are given for the rostrum (R), dorsal fin (D) and fluke (F) for each gait.
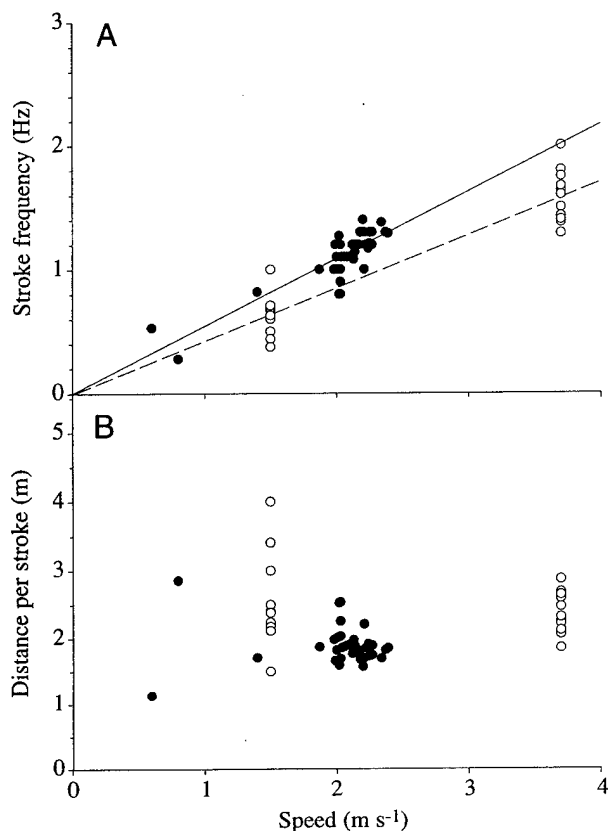
Fig. 2. Stroke frequency (A) and distance traveled per stroke (B) in relation to swimming speed for bottlenose dolphins. Data for instrumented (filled circles) and uninstrumented (open circles) dolphins are compared. Solid and dashed lines denote the least-squares linear regressions through the data points. Regressions for stroke frequency show a significant difference between the instrumented and uninstrumented animals ($P<0.05$). The distance moved per stroke was independent of speed in both groups of dolphins. Equations for the regression lines are given in the text.

with and without instrumentation showed linear increases in stroke frequency (f) with speed (v), but differed in the magnitude of the response. The regression for uninstrumented dolphins was:

$$f = 0.43v \qquad (3)$$

($N=30$, $r^2=0.90$, $P<0.05$), where stroke frequency is in strokes s^{-1} (Hz) and speed is in m s^{-1}. The stroke frequency of the instrumented dolphin was approximately 27 % higher at comparable speeds to the uninstrumented dolphins and was described by the equation:

$$f = 0.54v \qquad (4)$$

($N=41$, $r^2=0.73$, $P<0.05$). The distance traveled per stroke (Fig. 2B) did not change significantly with speed over the range tested for either the instrumented ($r^2=0.008$, $N=41$) or uninstrumented ($r^2=0.01$, $N=30$) dolphins. The mean distance per stroke was approximately 0.5 m (27 %) less for the instrumented dolphin than for uninstrumented dolphins swimming at comparable speeds.

Glides

Dolphins incorporated short (3–14 m) and long (>14 m) glide sequences during activity. Short glides occurred at the end of every ascent or descent, as the dolphin came to a stop or changed direction. Ascent glides ranged from 6 to 14 m in distance traveled (mean 9.3±2.5 m, $N=28$) and showed a mean deceleration of 0.07±0.12 m s^{-2} ($N=10$). Uninstrumented dolphins also demonstrated short periods of gliding associated with burst-and-glide propulsion during both horizontal submerged swimming and diving. These resulted in brief periods of deceleration before stroking resumed. The instrumented dolphin limited burst-and-glide propulsion to diving periods. We attribute the absence of burst-and-glide activity during horizontal swimming to the added drag of the instrument package. Long-distance gliding was an important component of the descent phase of dives for all dolphins. Glide distance varied with depth as described below.

Variations in gait

In addition to the three distinct gaits described above, dolphins utilized several variations of these patterns. Small-amplitude strokes (<20 % of body length) occurred intermittently as animals made the transition between active swimming and gliding. These smaller strokes also occurred between periods of medium-amplitude stroking. A variety of braking motions that included holding the fluke up, down or to either side were used by dolphins to decelerate.

Locomotor mode during swimming and diving

Horizontal swimming

Horizontal swimming by dolphins near the water surface or submerged at 5–16 m involved similar locomotor modes. For horizontal distances less than 15 m, the dolphins initially accelerated using large-amplitude strokes, followed by a period of decreasing stroke amplitude and finally passive gliding to the end point. The initial acceleration enabled the dolphins to reach speeds of 2.0–3.5 m s^{-1} in less than 2 s. Longer periods of steady-state swimming on the water surface at 1.5–3.7 m s^{-1} were accomplished by medium-amplitude stroking. Glide periods during steady-state swimming rarely exceeded 2 s.

Shallow dives

All shallow dives matched one of the following patterns with minor variation. Dives to 12 m by uninstrumented dolphins began with one or two large-amplitude strokes, resulting in a travel speed of 2.0 m s^{-1}. Starting at a depth of 4–6 m, the animals glided for approximately 5 m before braking or veering into a horizontal glide. Because of the short distance involved, the dolphins were able to glide to the surface after one or two medium-amplitude strokes at the start of the ascent. Dives to 16 m by the instrumented dolphin also began with a short period of active stroking followed by a short glide. The dolphin actively swam downwards for 9.0±1.9 m ($N=10$) before gliding the remaining 7.1±1.9 m ($N=10$). After braking, the dolphin used large-amplitude strokes to begin the ascent. Medium-amplitude strokes were used throughout the mid portion of the
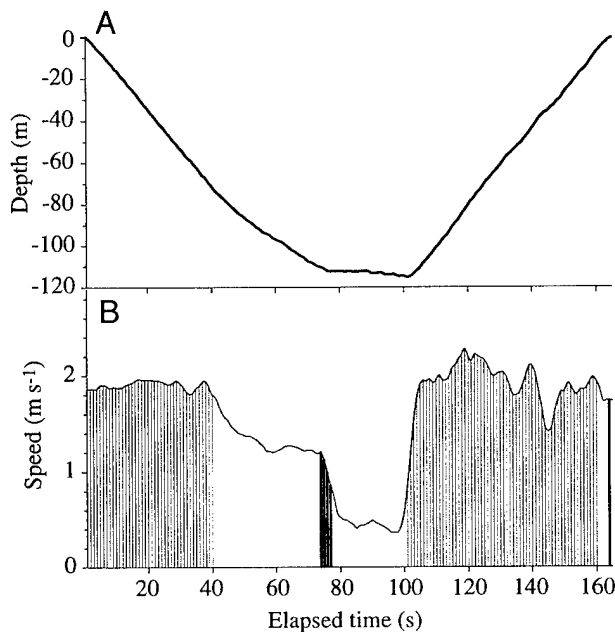
Fig. 3. Representative changes in depth (A) and speed and stroke pattern (B) in relation to dive time for an instrumented dolphin. Maximum dive depth was 112 m. Grey bars denote periods of stroking in which glide periods were less than 1 s in duration. Open areas show periods of continuous gliding or stationing. Black bars indicate braking at the end of the descent and ascent. Note the change in deceleration at 60 s midway through the gliding decent.
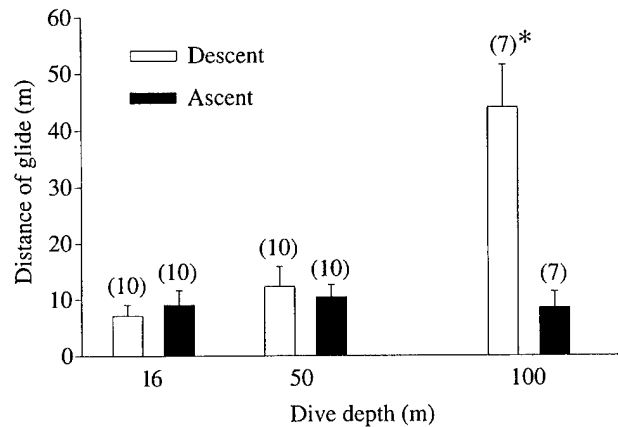

Fig. 4. Glide distance during descent (open columns) and ascent (filled columns) segments of dives in relation to depth for bottlenose dolphins. The height of the columns and lines shows the mean value +1 s.e.m. Numbers in parentheses indicate the total number of dives examined. An asterisk indicates a significant difference between the descent and ascent values for 100 m dives. Glide distances were not significantly different (at $P<0.05$) between ascent and descents for dives ranging from 16 to 50 m. In contrast, significant differences (at $P<0.001$) were found between glide distances for the descent and ascent segments of the 100 m dives.

ascent. As the dolphins approached the surface, stroke amplitude decreased to zero, with the dolphin gliding the remaining 9.1 ± 2.6 m ($N=10$).

Deep dives

The instrumented dolphin performed ten dives to depths of 50 m and eight dives to depths of 100–112 m. As observed for shallow dives, the dolphin used large-amplitude strokes to begin the descent, followed by medium-amplitude stroking. Intermittent stroking patterns incorporating short periods of gliding between active stroking often occurred during deep dives (Fig. 3). These periods of intermittent propulsion were characteristic for descents and ascents of deep dives but were not observed for shallow dives.

The percentage of time spent gliding during descent changed with depth for the diving dolphins. During 50 m dives, the dolphin glided for 30.3 ± 2.8 % ($N=10$) of the descent. This increased significantly (at $P<0.001$) to 51.2 ± 3.3 % ($N=8$) during the 100–112 m dives.

Glide distance for the 50 m dives, 12.3 ± 3.6 m ($N=10$), was not significantly different (at $P=0.21$) from the average for 16 m dives. However, glide distance during the descent increased significantly ($P=0.01$) with dive depths greater than 50 m. The total length of the glide was 43.6 ± 7.0 m ($N=8$) during 100–112 m dives (Fig. 4). Glides occurring during the ascent showed no significant changes with depth ($P=0.27$).

The speed of the dolphins during diving was correlated with

gliding or stroking periods. An example is shown in Fig. 3. During stroking on the descent of a 112 m dive, the speed of the dolphin was approximately 1.9 m s^{-1}. Cessation of stroking resulted in a period of deceleration that was followed by a constant speed of 1.2 m s^{-1} during the remainder of the descending glide. Speed during the ascent was more variable and corresponded with burst-and-glide activity (Fig. 3).

As with shallower dives, a braking motion occurred at the end of descent, followed by large-amplitude strokes at the beginning of ascent. Average glide distance to the surface was 10.4 ± 2.2 m ($N=10$) on 50 m dives and 8.5 ± 2.9 m ($N=8$) on 100–112 m dives.

Drag and buoyant forces

The drag of the dolphins increased significantly with speed and was comparatively higher for the instrumented dolphin (Fig. 5). The least-squares curvilinear regression for the instrumented dolphin was:

$$D = 1.78 + 8.93v^{2.99} \qquad (5)$$

($r^2=0.64$, $P=0.220$, $N=6$). The regression for uninstrumented dolphins was:

$$D = 4.15v^{2.00} \qquad (6)$$

($r^2=0.65$, $P=0.097$, $N=5$), where drag (D) is in newtons and speed (v) is in m s^{-1} for both equations.

For deep-diving dolphins, measured deceleration during gliding changed with depth because of changes in buoyant force. For example, the mean depth during prolonged (>2 s) descending glides was 67.5 ± 23.0 m, with a glide speed of 1.5 ± 0.3 m s^{-1} and a mean deceleration of 0.03 ± 0.06 m s^{-2}
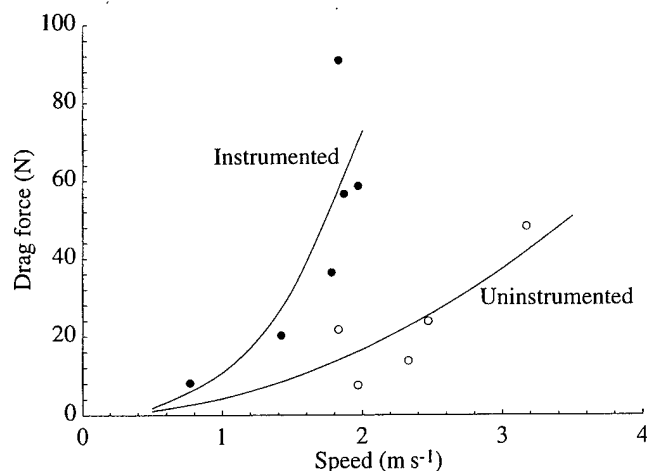
Fig. 5. Body drag in relation to horizontal glide speed for instrumented (filled circles) and uninstrumented (open circles) bottlenose dolphins. Solid lines denote the least-squares curvilinear relationships through the data points. All glide sequences took place at depths greater than three body diameters below the water surface to avoid surface wave effects. Speed represents the mean speed during each glide sequence. Equations for the relationships are given in the text.

(N=27 glide sequences). The decelerating force acting on vertically diving dolphins, calculated from the product of deceleration (0.03 m s^{-2}) and the mass of the instrumented dolphin including entrained water (202 kg), was 6.1 N. This compares with a drag of 31.8 N for gliding dolphins moving horizontally at the same speed (Fig. 5; equation 5). Presumably, the drag of the vertically diving dolphin was countered by a downward force of 25.7 N (31.8–25.7=6.1) (Table 3). Similar calculations for the ascent phase demonstrate the positive effect of buoyancy as a dolphin nears the water surface. The mean depth of gliding for ascent from instrumented dives was 5.5±2.2 m, with a mean speed of 1.6±0.2 m s^{-1} and deceleration of 0.07±0.12 m s^{-2} (N=10). The

product of deceleration and mass is 14.1 N for the dolphins on a vertical ascent. In comparison, the calculated drag for horizontally gliding dolphins moving at 1.6 m s^{-1} is 38.4 N (equation 5). Thus, the final ascent drag was countered by an upward buoyant force of 24.3 N (38.4–24.3=14.1).

From these calculations, we find that the buoyant force acting on the diving dolphins in this study changed from +24.3 N near the water surface (5.5 m depth) to –25.7 N at a depth of 67.5 m, a difference of 50.0 N. This is equivalent to a change in water displacement of 5.1 l (50.0 N/9.8 m s^{-2}=5.1 kg or approximately 5.1 l of water). Such a change in displacement is reasonable since dolphins dive following inspiration and air compresses with depth. From equation 1, an initial lung volume of 8–10 l would be needed to achieve this magnitude of volume change in the diving dolphin, which is within the reported range for a 177 kg dolphin (Ridgway et al., 1969; Stahl, 1967).

Fig. 6 illustrates the changes in buoyant force of 8.5 l of air with depth for diving dolphins. This curve and the calculated buoyancy of the dolphin differed consistently by 33.2 N, and we assume that this was due to the weight of the dolphin's body. Thus, for the instrumented dolphin, diving with a lung volume of 8.5 l, equation 2 becomes:

$$B_D = 83/(1 + 0.1h) - 33.2,\qquad(7)$$

where B_D is the buoyant force in newtons at depth h in m, 83 N is the buoyant force of 8.5 l of air and –33.2 N is the buoyancy of the dolphin's body without air. The net force acting on the gliding dolphin can then be calculated from the difference between this buoyant force and total body drag (Fig. 5).

The above calculations are appropriate for gliding dolphins in which swimming motions are absent. To calculate the drag on swimming dolphins, we need to account for the additional drag due to locomotor movements. A conservative estimate of this active drag is three times that of the gliding animal (Lighthill, 1975, 1971; Webb, 1975, 1984; Williams and Kooyman, 1985; Fish, 1993).

Table 3. *Locomotor variables, total body drag and buoyant forces for a bottlenose dolphin during a 100 m dive*

	Deceleration (m s^{-2})	Speed (m s^{-1})	Net force (N)	Drag (N)	Buoyancy (N)	Depth (m)
Descent glide	0.03±0.06 (27)	1.5±0.3 (27)	6.1	31.8	–25.7	67.5
Ascent glide	0.07±0.12 (10)	1.6±0.2 (10)	–14.1	–38.4	24.3	5.5
Descent swimming		1.7±0.0	160.6	136.3	24.3	5.5
Ascent swimming		1.9±0.0	–213.6	–187.9	–25.7	67.5

Gliding and swimming during ascent and descent are compared.

Deceleration, speed and depth were measured for a dolphin wearing an instrument pack.

Net force, drag and buoyancy were calculated as described in the text. Drag calculations for swimming on ascent and descent include an active drag factor of 3 (Fish, 1993; Lighthill, 1971, 1975; Webb, 1975, 1984) to account for the additional drag associated with swimming movements.

All downward forces relative to the water surface are indicated by a negative sign.

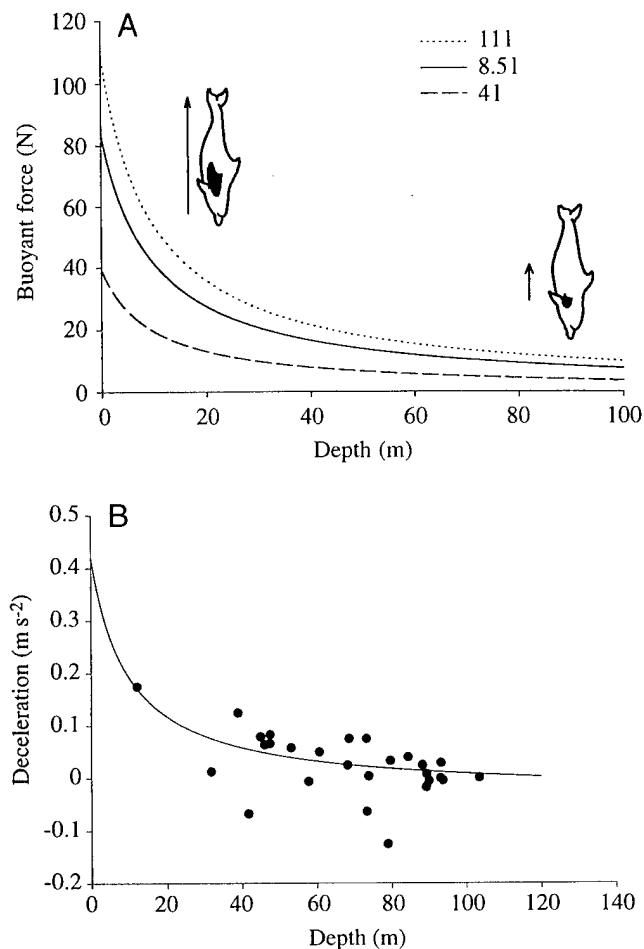Numbers in parentheses indicate N for the measured variables.

Fig. 6. Changes in the buoyant force of lung air (A) and deceleration (B) in relation to dive depth in bottlenose dolphins. Calculations for buoyant force are based on equations presented in the text and are compared for three different initial lung volumes. Note the rapid decline in buoyant force with depth as the water pressure progressively collapses the lungs. The decline in deceleration of gliding dolphins (B) determined from video analyses paralleled that calculated for buoyant force. Each point represents an individual glide sequence. The solid line in B is not a regression for the data, but rather the calculated deceleration based on buoyancy changes with depth (see text).

Effects of instrumentation

Average speeds during diving and horizontal swimming were 9–10 % lower for the instrumented dolphin than for uninstrumented dolphins. Drag was 3.3 times higher for the instrumented dolphin at the mean gliding speed of $1.47\,\mathrm{m\,s^{-1}}$ (Fig. 5). The elevated drag resulted in a 27 % reduction in distance achieved per stroke and a concomitant increase in stroke frequency (Fig. 2). Although stroke amplitude appeared to be higher for the instrumented dolphin, differences in measurement techniques for instrumented and uninstrumented animals prevented accurate comparisons. Because of the demonstrated effects of the instrumentation on drag and swimming mechanics, the glide distances reported here should be considered as conservative estimates of the true performance of uninstrumented dolphins performing deep dives.

Discussion

The importance of gait transitions during swimming and diving

Foraging aquatic mammals must divide their time between two important resources, oxygen located at the water surface and prey items located at depth (Dunstone and O'Connor, 1979). The swimming modes selected by mammals moving between these resources will affect their locomotor efficiency and, ultimately, the cost/benefit relationships for foraging. Previous studies with dolphins have shown that elevating swimming speeds during ascent and descent to decrease the duration of a dive leads to an extraordinarily rapid depletion of limited oxygen reserves (Williams et al., 1993). Travel too slowly, however, and time becomes limiting as basal metabolic demands exhaust the available oxygen (Williams et al., 1999).

Data from the present study demonstrate that bottlenose dolphins tailor their swimming patterns to diving depth, a strategy that leads to energetic efficiency (Figs 3, 4). As found for running animals (Heglund et al., 1974; Taylor, 1978; Hoyt and Taylor, 1981), changes in gait by swimming and diving dolphins were associated with specific tasks and speeds (Table 2; Fig. 3). Dolphins switched gaits primarily in conjunction with acceleration needs. During initial acceleration from rest, stroke frequencies and fluke amplitudes often exceeded those used during steady swimming. Large-amplitude movements of the head and back accompanied these large fluke motions. The tip of the rostrum showed an excursion of nearly 20 % of body length, while fluke amplitude exceeded 40 % of body length (Table 2). As the dolphin's speed increased, stroke amplitude gradually decreased to the values observed during steady-state swimming. These results are consistent with models that predict increased mechanical efficiency during low-speed swimming when thrust is produced by accelerating a large mass of fluid (per time) to a low velocity instead of accelerating a small mass to a high velocity (Alexander, 1977).

During diving, dolphins minimized the use of large-amplitude strokes and incorporated prolonged glide periods as speed and coincident drag increased. Large-amplitude strokes only occurred for brief (<5 s) periods during the initial descent and ascent. Except for these initial periods, diving dolphins relied on medium-amplitude strokes and, when possible, even smaller stroking movements. The smaller-amplitude strokes occurred during transitions between steady-state stroking and gliding, with stroke frequency remaining unchanged. These results are not surprising when the hydrodynamics are considered. High-amplitude movements are a departure from the streamlined shape of the dolphin and theoretically result in elevated levels of drag, especially as stroke amplitude is increased (Fish et al., 1988; Lighthill, 1971; Webb, 1975). An actively swimming animal may encounter a three- to fivefold increase in total body drag over gliding values as a result of

elevated pressure drag (Fish et al., 1988), separation or thinning of the boundary layer (Lighthill, 1971) and increased drag from thrust production (Webb, 1975). The marked effect of even small adjustments in posture on drag and forward movement of the dolphin was observed when an animal used braking movements to reduce speed. Raising the fluke a distance equivalent to 10 % of body length resulted in an 11.5-fold increase in total body drag.

Although prolonged gliding allows diving dolphins to avoid active drag, it places a limit on maintaining propulsion. To circumvent this, dolphins and other swimmers often rely on a burst-and-glide style of swimming that incorporates short periods of stroking during prolonged glide sequences to maintain forward speed (Videler, 1981; Videler and Weihs, 1982; Weihs, 1974). Despite elevated drag associated with re-acceleration between glides, the calculated energetic cost for this interrupted mode of swimming is significantly lower than for continuous swimming (Blake, 1983).

Because dolphins produce power by oscillating their flukes (Lang and Daybell, 1963; Slijper, 1961; Videler and Kamermans, 1985), the mass of the fluke plus entrained water must be decelerated to a stop then re-accelerated in the opposite direction both at the top and bottom of each stroke. The alternate storage and release of elastic energy in conjunction with fluke movements could serve as a potential energy-conserving mechanism. Changes in the axial body of the swimming dolphin are qualitatively similar to those of galloping terrestrial mammals in which the trunk is used as a spring to store elastic energy (Taylor, 1978). Several spring-like tissues have been implicated as energy-saving mechanisms for swimming dolphins. Pabst (1990) described a crossed, helically wound, fiber array encasing the dolphin body. The fiber array, derived from ligaments, muscle tendons and blubber tissue, gains rigidity because of the tension it is under. This array may act as a spring, storing energy during part of the stroke cycle and recovering it during the remainder (Pabst, 1990). Although intriguing, such elastic storage mechanisms have yet to be tested in a freely swimming dolphin and warrant further investigation.

The swimming mechanics of dolphins share other features common to terrestrial animals and swimming humans. In terrestrial mammals, stride frequency increases linearly with speed during walking and trotting. As speed increases, many runners switch to a gallop in which speed is achieved by lengthening the stride rather than by increasing stride frequency (Heglund et al., 1974). Conversely, human swimmers decrease the distance per stroke (the aquatic equivalent of stride length) and increase the stroke frequency to achieve greater speeds (Costill et al., 1991). Horizontally swimming dolphins combine both patterns and increase stroke frequency linearly with speed while the distance per stroke remains relatively constant (Fig. 2). Mean distance per stroke was 2.4 m irrespective of speed. Stroke amplitude in dolphins also remained constant during horizontal swimming, with amplitude remaining at 20 % of body length for steady speeds ranging from 1.2 to 6.0 m s^{-1} (Table 2; Fish, 1993).

Buoyancy, gliding and energy expenditure during diving

Locomotor performance by horizontally swimming and vertically diving dolphins is influenced by very different physical factors. During horizontal swimming near the water surface, dolphins encounter high levels of drag associated with wave generation (Hertel, 1969). The effects of wave drag are negligible for diving dolphins once the animal is three body diameters below the water surface. Diving dolphins, however, face unique changes in buoyant forces with depth that become a major influence on performance and behavior.

An interesting finding in this study was the use of prolonged periods of gliding by dolphins for dives exceeding a depth of 50 m. Approximately 50 % of the descent phase was spent gliding rather than actively swimming on dives to a depth of 100 m. Deceleration rate decreased progressively during prolonged glides, finally reaching a point of zero deceleration at a depth of 90 m (Fig. 6B). These extended glides occurred only during the descent phase of deep dives (Fig. 4), suggesting that physical factors rather than distance *per se* dictated glide performance. Changes in buoyancy with depth due to lung compression from increased pressure probably contributed to these results. In general, dolphins dive after inspiration and exhale upon surfacing, indicating that they dive with inflated lungs (Ridgway et al., 1969; present study). Goforth (1986) reported that the diving lung volume of dolphins was approximately 75 % of maximum lung volume. The bronchi and trachea as well as the alveoli of the cetacean lung are collapsible, as determined in pressure chamber tests. Only the bony nares, with a volume of 50 ml, are rigid (Ridgway et al., 1969). Such a morphological structure permits a progressive collapse of the thorax with increased pressure at depth.

Compression of the air spaces in dolphins decreases volume without an accompanying reduction in mass. As a result, the dolphin becomes less buoyant with depth. Although it was not possible to measure directly the volume of air in an actively diving dolphin, the range of lung volumes and their effect on buoyancy have been determined for excised lungs from a 200 kg bottlenose dolphin (Ridgway et al., 1969). Ridgway and Howard (1979) calculated that alveolar collapse is complete once bottlenose dolphins experience pressures equivalent to 65–70 m in depth. The theoretical changes in buoyant force associated with this collapse are shown in Fig. 6. The maximum respiratory volume of the dolphin (11 l) was associated with neutral to slightly buoyant forces at full inflation and with a negative buoyancy of 10 kg when the lungs were deflated. In the present study, we found that changes in the deceleration rate of gliding dolphins were similar in pattern to the calculated changes in buoyant forces with lung compression (Fig. 6), suggesting a correlation between pressure and locomotor movements at depth.

Using this basic information, we can examine the relationship between physical factors and the swimming behavior of dolphins during diving. Major physical forces include buoyancy, acting in an upward or downward direction depending on diving depth, and drag opposing the forward

Table 4. *Calculated energetic costs for overcoming drag and buoyancy during a 100 m dive by an adult bottlenose dolphin*

	Active swim distance (m)		Speed (m s^{-1})		Locomotor cost (J)
	Descent	Ascent	Descent	Ascent	Total
Measured	53	92	1.73	1.90	26 064
Neutral buoyancy					
Total time-fixed	95	95	1.76	1.76	28 608
Speed-fixed	95	95	1.73	1.90	31 465

Locomotor costs were determined from the product of net forces (Table 3) and distance traveled.

Measured values for a dolphin wearing an instrument package are compared with those for two models assuming neutral buoyancy. The time-fixed model maintains the total dive time to that measured for the diving dolphin. Swimming speed is adjusted to accommodate the time requirement. The speed-fixed model maintains the swimming speeds for ascent and descent to those measured for the diving dolphin. However, the duration of the dive is adjusted to accommodate the neutral buoyancy and speed requirements.

movement of the dolphin. For the straight-line trained dives in the present study, total body drag acts upwards as the animal descends and downwards relative to the motion of the dolphin during ascent. The combined effects of these forces during various segments of a 100 m dive by a bottlenose dolphin are presented in Table 3. For the instrumented dolphin, passive gliding predominated when the calculated net force opposing the animal was less than 21 N. If the opposing force was higher, prolonged gliding was untenable and the dolphin switched to either stroking or short periods of burst-and-glide swimming. This may explain in part the high proportion of gliding during vertical diving in comparison with horizontal swimming by the same animal. With no buoyancy advantage during horizontal swims, the calculated drag for the speed range examined exceeded 21 N, and little gliding occurred. As mentioned above, descending glides during long descents reached zero deceleration at depth of approximately 90 m depth. At this depth, the downward force imparted by negative buoyancy fully counteracted the calculated drag and provided the dolphin with a theoretical 'free ride'.

Although the progressive negative buoyancy with depth provides a locomotor advantage during descent, the reverse occurs during ascent. The same force that pulled the dolphin down must be overcome for the animal to return to the surface, seemingly negating any benefit. If energetic and hydrodynamic factors are considered together, we find that gliding provides an overall advantage for the diver. This is due to a significant reduction in active drag, which contributes to the energetic efficiency of burst-and-glide swimming (Blake, 1983). The locomotor behavior of diving dolphins is analogous to a type of burst-and-glide swimming, with exceptionally long glides facilitated by changes in buoyancy with depth.

The energetic advantage of gliding may be determined theoretically by calculating the total energy expended to

overcome drag and buoyancy (locomotor cost) in diving dolphins. We estimated locomotor costs from the product of the net forces and mean distance covered during gliding and swimming (Tables 3, 4). On the basis of the straight-line dives examined in this study, the locomotor cost for an instrumented dolphin performing a 100 m dive was 26 064 J (0.74 J kg^{-1} m^{-1}). This compares with a minimum locomotor cost of 0.73 J kg^{-1} m^{-1} calculated from the difference between maintenance costs and total minimum cost of transport for bottlenose dolphins swimming near the water surface (Williams et al., 1992; Williams, 1999). In view of the similarity in locomotor costs between these swimmers and divers, it is apparent that deep-diving dolphins select energetically efficient modes of locomotion. Despite the effect of the instrumentation (Figs 2, 5), the diving dolphins in the present study were able to match the predicted minimum locomotor costs of swimming dolphins by taking advantage of changes in buoyancy. The theoretical costs are considerably higher if we assume that dolphins are neutrally buoyant throughout the dive. If a dolphin were neutrally buoyant and tried to maintain the same dive duration for a 100 m dive, as measured in this study, then locomotor costs would increase by 10 %. A neutrally buoyant dolphin maintaining the same swimming speeds (with a consequent shorter dive duration) for a 100 m dive experiences a 21 % increase in energetic requirements (Table 4).

The reduction in active drag during gliding was the primary factor leading to the energetic savings during diving rather than changes in buoyancy *per se*. Because of the marked influence of the instrument package on body drag (Fig. 5), these calculations admittedly represent a conservative estimate of the effects of buoyancy on gliding performance. It is likely that uninstrumented dolphins will exhibit even greater gliding performance with potentially greater energetic savings than indicated in these calculations. The reduction in power requirements and hence energetic costs associated with gliding initially appears modest. However, the savings may provide a significant advantage to free-ranging dolphins by allowing extended foraging time through the conservation of limited energy stores.

In conclusion, the present study illustrates how the interrelationships between swimming mechanics, buoyancy and underwater behavior support energetically efficient locomotion in diving dolphins. Similar conclusions regarding buoyancy and performance have been reached for other marine animals, including free-ranging elephant seals (*Mirounga augustirostris*) (Webb et al., 1998), diving ducks (Lovvorn et al., 1991) and a variety of fish species (Alexander, 1990). Variation in glide performance facilitated by changes in buoyancy appears to be an important mechanism that enables marine mammals to conserve limited oxygen stores during submergence. A corollary to this study suggests that speed alone is a relatively poor indicator of aquatic effort and may be inadequate for assessing energetic costs in diving marine mammals. Both gliding and active swimming often occur at similar speeds. However, the energetic consequences of each may be very different.

This series of papers on the diving physiology of dolphins was inspired by the work of Gerald L. Kooyman; they are dedicated to him in celebration of his remarkable research career and influence on all comparative physiologists. This study was supported by an Office of Naval Research grant and ASSEE fellowship (N00014-95-1-1023) to T.M.W. The authors thank the many people that assisted in this study including the trainers and dolphins at the SPAWAR facility in San Diego and the Dolphin Experience in the Bahamas. Computer assistance by S. Collier at Texas A&M University is gratefully acknowledged. In addition, the authors appreciate the critical evaluation of this manuscript by S. Noren, D. Noren and S. Kohin and lively discussions with F. Fish. All experimental procedures were evaluated and approved according to animal welfare regulations specified by NIH guidelines. UCSC and SPAWAR Systems Center (San Diego) conducted institutional animal use reviews.

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ORIGINAL PAPER

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Thermoregulation during swimming and diving in bottlenose dolphins, *Tursiops truncatus*

Abstract Heat transfer from the periphery is an important thermoregulatory response in exercising mammals. However, when marine mammals submerge, peripheral vasoconstriction associated with the dive response may preclude heat dissipation at depth. To determine the effects of exercise and diving on thermoregulation in cetaceans, we measured heat flow and skin temperatures of bottlenose dolphins (*Tursiops truncatus*) trained to follow a boat and to dive to 15 m. The results demonstrated that skin temperatures usually remained within 1 °C of the water after all exercise levels. Heat flow from peripheral sites (dorsal fin and flukes) increased over resting values immediately after exercise at the water surface and remained elevated for up to 20 min. However, post-exercise values for heat flow from the flukes and dorsal fin decreased by 30–67% when dolphins stationed at 15 m below the surface. The pattern in heat flow was reversed during ascent. For example, mean heat flow from the flukes measured at 5 m depth, 40.10 ± 2.47 W·m^{-2}, increased by 103.2% upon ascent. There is some flexibility in the balance between thermal and diving responses of dolphins. During high heat loads, heat transfer may momentarily increase during submergence. However, the majority of excess heat in dolphins appears to be dissipated upon resurfacing, thereby preserving the oxygen-conserving benefits of the dive response.

Introduction

The high thermal conductivity and heat capacity of water poses a unique thermoregulatory challenge for active marine mammals that differs from that of terrestrial mammals. During exercise, terrestrial mammals increase both heat production and muscle blood flow (Mitchell 1977). Excess heat generated by the active muscles during exercise may be dissipated by increased blood flow through dilated vessels of the skin (Berger 1982; Franklin et al. 1993; Kellogg et al. 1993). Ultimately, the heat is transferred to the surrounding environment by four different pathways, conduction, convection, radiation, and/or evaporation (Mitchell 1977; Berger 1982; Brooks and Fahey 1984). In comparison, the primary thermal adaptation in phocid seals and cetaceans is a thick blubber layer that insulates against heat loss to the water (Kanwisher and Sundnes 1966; Irving 1969; Ryg et al. 1993). Poorly insulated peripheral areas are utilized as thermal windows which permits the transfer of excess heat via conduction and convection during exercise or when ambient water is warm (McGinnis et al. 1972; Kanwisher and Ridgway 1983).

To limit heat transfer at the peripheral sites, cetaceans maintain a counter-current arrangement of vessels in their fins and flukes (Scholander and Schevill 1955; Hampton and Whittow 1976). During periods of elevated activity, however, the counter-current heat exchanger is bypassed and blood flow through superficial veins near the skin increases to provide maximum cooling (Scholander and Schevill 1955). Cetaceans take advantage of cooled blood from these peripheral sites to

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regulate temperature-sensitive organs such as the intra-abdominal testes (Rommel et al. 1992, 1994; Pabst et al. 1995).

Little is known about the use of these specialized thermal windows during different levels of activity in cetaceans. Previous studies have telemetered deep body temperatures of bottlenose and Hawaiian spinner dolphins during rest, surface swimming, and leaps and spins in pools (Hampton et al. 1971; McGinnis et al. 1972; Hampton and Whittow 1976; Whittow 1987). Heat flow and skin temperatures (T_s) of Hawaiian spinner dolphins during rest (McGinnis et al. 1972; Hampton and Whittow 1976) and an Atlantic bottlenose dolphin exercising in a pool (Hampton et al. 1971) have also been investigated. As expected, activity resulted in an increase in deep body temperature of Hawaiian spinner dolphins (Hampton and Whittow 1976; Whittow 1987) and a Pacific bottlenose dolphin (McGinnis et al. 1972). Heat flow from the tip of the pectoral fin of the Atlantic bottlenose dolphin increased three to four-fold after swimming at a speed of 1 m·s^{-1} for 6–7 min (Hampton et al. 1971), presumably to counteract an increase in core temperature with activity. Variation in heat flow from different regions of the body was considerable (Hampton et al. 1971; Hampton and Whittow 1976), however, as was variation in heat flow between animals (Hampton and Whittow 1976). In contrast, external T_s at all measurement sites were fairly uniform and greater than, but within 1 °C, of the surrounding water temperature (Hampton et al. 1971; Hampton and Whittow 1976).

The details of cetacean thermoregulation during swimming and diving in the open ocean remain unknown. Because blood flow to peripheral regions is reduced during diving to conserve total body oxygen (Scholander 1940), the amount of blood available for heat dissipation at peripheral thermal windows may be compromised during subsurface activity. Thus, there appears to be a direct conflict between the cardiovascular requirements for thermoregulatory and diving responses in marine mammals (Whittow 1987).

This study examines thermoregulation in active bottlenose dolphins in the open ocean. Specifically, changes in heat flow and T_s were measured for swimming and diving animals. By conducting the studies under warm water conditions in the Bahamas we were able to investigate mechanisms for dissipating excess heat in an environment that poses a thermoregulatory challenge. To determine the effects of the dive response on post-exercise heat transfer, we compared the levels of heat flow for animals stationed at the water surface and submerged. The results of the study demonstrate that heat flow increases at peripheral thermal windows in response to increased swimming activity. However, this response is attenuated when the animal is diving. Rather than challenge the dive response, dolphins are able to delay the dissipation of excess heat until the post-dive recovery period.

Materials and methods

Animals

Three adult Atlantic bottlenose dolphins (*Tursiops truncatus*) were used in these studies (Table 1). Blubber thickness was measured on the flank by a portable ultrasound unit (Scanoprobe II) to assess the general condition of insulation for each animal. The animals were housed in large (15 m × 15 m × 4 m deep), salt-water pens connected to the open ocean via a channel near Port Lucaya, Grand Bahama Island. All animals were acquired from the wild and had been maintained at the facility for over 8 years.

The dolphins were fed daily a diet of capelin and herring supplemented with multi-vitamins (Sea Tabs, vitamin C, B-12, and B complex). Mean water temperature (T_w) during the experimental period from August through mid-September was 29.8 °C; mean air temperature (T_a) was 28.6 °C.

Experimental design

Local T_s and heat flows of two dolphins were measured under three conditions: (1) during rest on the water surface, (2) post-exercise on the water surface, and (3) post-exercise at a dive depth of 15 m. To assess temporal changes in the thermoregulatory response during a dive, we measured heat flow continuously as one dolphin ascended from a depth of 5 m to the water surface. Measurement sites for heat flow and T_s (Fig. 1) were chosen to include peripheral thermal windows (dorsal fin and fluke blade) and a well insulated region of the body (flank).

Resting measurements were made on two male dolphins trained to float next to a deck prior to exercise sessions. The effects of exercise on heat flow and T_s were also determined on these two dolphins. Post-exercise measurements were taken as the animals stationed on the water surface immediately following a 12–22 min swim at 3.7 m·s^{-1} or an 11–13 min swim at 4.3 m·s^{-1}. Additional measurements were taken during the recovery period at 10-min intervals for up to 30 min following the cessation of swimming.

During swimming, the dolphins remained on or near the water surface and matched their swim speed to that of a 5-m Boston whaler. Brief periods (< 1 min) of wave-riding in the bow or stern wake were observed. Speed of the boat was determined by videotaping (Sony Handicam Hi 8) a known distance between two fixed points as the boat was running at a constant RPM (revolution per minute). The range of speeds in this study (3.7–4.3 m·s^{-1}) were determined by digital analysis of the video tape (Peak Performance software) and the calculated relationship between RPM and timed distances. The two swim speeds used in this study were well above the minimum cost of transport speed of 2.1 m·s^{-1} determined for bottlenose dolphins (Williams et al. 1992, 1993) and were considered moderate to high exercise loads for these animals.

The effect of the dive response on post-exercise heat flow and T_s was determined by repeating the measurements on dolphins sta-

Table 1 Morphological characteristics of the bottlenose dolphins used in this study. Lengths are straight line measurements from the tip of the rostrum to the notch in the flukes. Mass was estimated from measured length and maximum circumference. Age was determined from approximate age at time of capture and duration of captivity. Blubber depths are mean values measured for the flank (see Fig. 1). (*F* female, *M* male)

Dolphin	Sex	Age (years)	Length (cm)	Mass estimate (kg)	Blubber depth Mean ± SE (mm)
1	M	14	252.0	227	11.8 ± 0.3
2	M	14	259.0	236	13.2 ± 0.3
3	F	14	238.0	172	12.0 ± 0.0

tioned at 15 m depth. The dolphins swam at 4.3 m·s^{-1} for 11–13 min, as above, to the dive site approximately 3 km offshore of Port Lucaya, Grand Bahama Island. At the dive site each dolphin accompanied a trainer to the sandy bottom. Measurements were taken from the three sites in a random order immediately upon the animal reaching the station position at 15 m. Generally, two anatomical sites were measured before the animal had to return to the surface to breathe. Measurements continued when the animals returned to the trainer.

To assess temporal changes in heat flow associated with the dive response without prior exercise, we continuously monitored heat flow from one female dolphin ascending from a 5-m dive. Steady-state measurements were recorded while the animal stationed at depth in a shallow channel and following the initial breath after ascent. Only the dorsal fin and fluke blade were measured during these experimental sessions. After the submerged measurement, scuba divers ascended with the dolphin, keeping the heat flow/thermistor probe fixed on the measurement site. One anatomical site was measured for each submergence and subsequent breath.

Heat flow

Heat flow across the skin of the dolphin to the water was measured with a 2.54-cm diameter circular model heat flux transducer (Thermonetics). The internal surface of the transducer was held underwater against the skin of the stationary animal until it stabilized and a steady state signal was recorded for more than 15 s. Most heat flow measurements required 1–2 min to complete. To ensure that ambient water flowed freely on the external side of the transducer, it was mounted on a spring and open pore PVC handle. Zero and range calibrations were conducted during each experimental session. Accuracy for the instruments was ±7.10–7.89 W·m^{-2} depending on the instrument used.

Voltage (mV) from the transducer was measured on a hand-held Auto Range Digital Multimeter (Radio Shack model no. 22-166A or Micronta model no. 22-166A). For measurements at depth, the multimeters were housed in a clear acrylic waterproof box (Ikelite). A 5-m line from the transducer probe handle was connected to the box by an underwater connector.

Skin temperature

T_s was determined using a thermistor implanted on the surface of the heat flow disk (Thermonetics). During dives, the thermistor was attached to a second multimeter which allowed continuous, simultaneous monitoring of T_s and heat flow. T_s from the thermistor was recorded when the heat flow value was stable. The thermistor was calibrated against a digital thermometer (Physitemp) in an insulated water bath prior to experiments. Calibration temperatures of the thermistor ranged from 18.6 °C to 36.6 °C and spanned the range of experimental temperatures. Accuracy was found to be within ±0.1 °C.
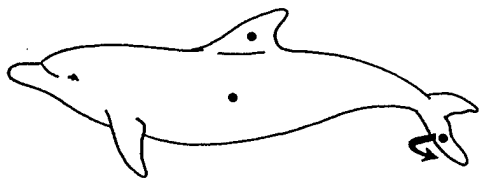

Fig. 1 Measurement sites for heat flow and skin temperature (T_s) of bottlenose dolphins. The *dots* designate the three sites (dorsal fin, flank, and the underside of the fluke blade) where the hand-held transducers were placed on the animals. Blubber thickness was measured on the flank only

Analyses

T_s and heat flow data were analyzed using Sigma Stat software (Jandel Scientific 1995) and were pooled when there were no significant differences in the data from individuals (t-tests: $P > 0.05$). One-way repeated measures ANOVA on ranks was used for the analyses of T_s data. One-way repeated measures ANOVA with Student-Newman-Keuls pairwise multiple comparison method was used for the analyses of heat flow data during rest on the water surface, post-exercise on the water surface, and post-exercise at depth. Significant changes in heat flow before and after a 5-m ascent from depth were determined from paired t-tests. Linear regressions were from least squares methods using Sigma Plot software (Jandel Scientific 1995) with significances determined through analysis of variance using Sigma Stat (Jandel Scientific 1995). All statistical results were deemed significant when $P \leq 0.05$. Means are presented as ±1 SE unless otherwise indicated.

Results

Skin temperature

T_s did not vary significantly between the two dolphins ($P > 0.05$); therefore, the results were pooled (Fig. 2). Values for T_s ranged from 28.74 °C to 31.61 °C and were correlated to T_w (Fig. 2).

Most T_s, irrespective of body site, remained within 1 °C of T_w during rest and throughout the post-exercise recovery period. In general, the lowest T_s were found for resting and post-exercise submerged dolphins when compared to post-exercise dolphins measured at comparable T_w on the water surface (Fig. 2). However, these differences were not significant ($P > 0.05$).
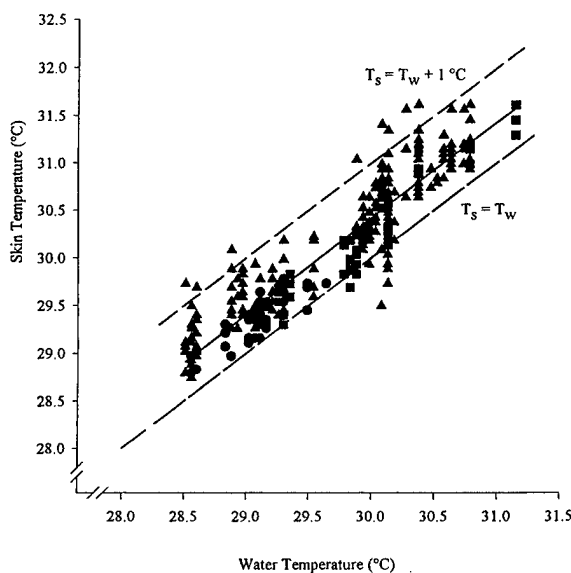

Fig. 2 T_s from three anatomical sites of two adult male bottlenose dolphins during rest on the water surface (■), post-exercise on the water surface (▲), and post-exercise submergence to 15 m (●). The *dashed lines* show T_s = ambient water temperature (T_w) and T_s = T_w + 1 °C. The *solid line* denotes the least squares regression through the data points. T_s was correlated to T_w according to the relation: T_s = 1.012 + 0.980 T_w ($n = 314$; $r^2 = 0.850$; $F = 1770.214$; $df = 1$; $P < 0.001$)

Heat flow on the water surface

Heat flow of dolphins resting on the water surface ranged from 7.89 $W \cdot m^{-2}$ to 134.13 $W \cdot m^{-2}$, and depended on both the animal and measurement site. Although differences in heat flow between the three sites were not significant, heat flow from the dorsal fin tended to be the highest (72.24 ± 9.63 $W \cdot m^{-2}$ for dolphin 1; 69.17 ± 4.91 $W \cdot m^{-2}$ for dolphin 2), while heat flow from the flank tended to be the lowest (50.85 ± 5.94 $W \cdot m^{-2}$ for dolphin 1; 43.15 ± 4.74 $W \cdot m^{-2}$ for dolphin 2).

All sites showed an increase in heat flow from rest following surface swimming at 3.7 $m \cdot s^{-1}$, with significant increases ($P < 0.05$) at the two thermal windows, the dorsal fin and fluke blade (Fig. 3). Heat flow from the dorsal fin was 2.2 times the resting value after 12 min of exercise and 2.5 times resting after 22 min of exercise. The maximum heat flow measured for this site was 180.38 ± 15.86 $W \cdot m^{-2}$ immediately after swimming for 22 min. Heat flow from the fluke blade was 1.9 times the resting heat flow value immediately after 12 min of exercise and 2.3 times resting immediately after 22 min of exercise. The maximum heat flow measured from the

fluke blade was 122.52 ± 12.93 $W \cdot m^{-2}$ immediately after swimming for 22 min. Heat flow from the peripheral sites remained significantly elevated above resting values for at least 10 min during recovery and usually did not decrease significantly below the initial post-exercise heat flow values until 20 min into the recovery period (Fig. 3).

Both peripheral sites showed significantly greater heat flow than the flank at 0 min ($F = 12.16$, $df = 2$, $P < 0.001$), 10 min ($F = 7.02$, $df = 2$, $P = 0.010$), and 20 min ($F = 10.23$, $df = 2$, $P = 0.002$) of recovery following a 12 min swimming bout. The trend was similar after 22 min of swimming but significant only for the dorsal fin.

Heat flow at depth

Diving immediately after an 11–13 minute swim at 4.3 $m \cdot s^{-1}$ resulted in a reduction in heat flow when compared to values measured on the water surface after the same exercise speed and duration. Reductions of 30–67% were observed from the two peripheral sites at depth for both dolphins (Figs. 4, 5). Heat flow from both the dorsal fin and the fluke blade were significantly lower during a post-exercise dive than during post-exercise on
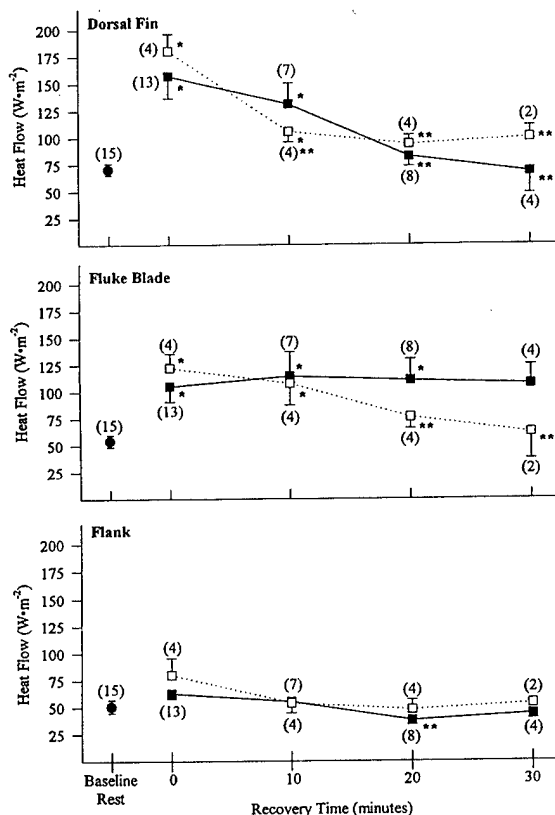

Fig. 3 Heat flow during post-exercise recovery in bottlenose dolphins. Heat flow from the dorsal fin, fluke blade, and flank during rest (●) and after 12 min (■) and 22 min (□) of swimming at 3.7 $m \cdot s^{-1}$ are presented. Values significantly greater than resting (*) and significantly less than 0 min post-exercise (**) are indicated. Data are pooled for two dolphins. Numbers in parentheses indicate the total number of trials. Mean values during the post-exercise recovery period are presented with SE bars in one direction only for clarity
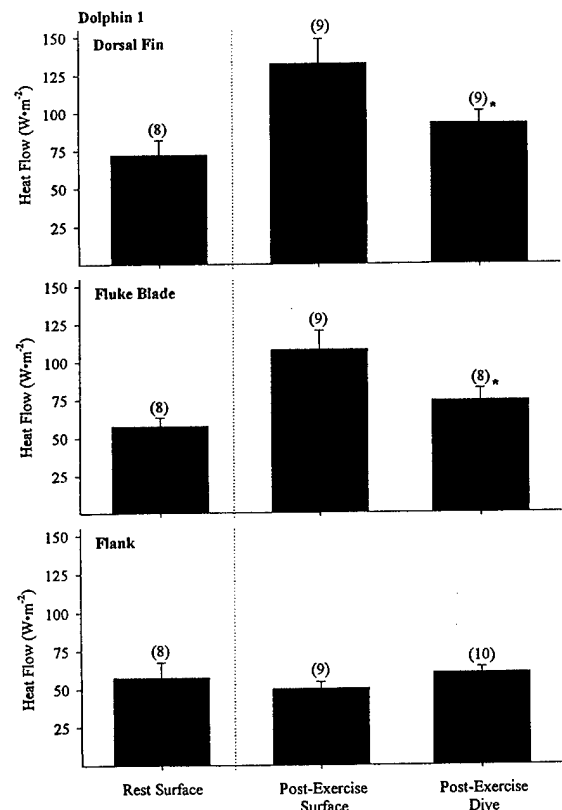

Fig. 4 Heat flow for three activity levels in dolphin 1. Post-exercise measurements at the surface and at 15 m depth were after 11–13 min of swimming at 4.3 $m \cdot s^{-1}$. Mean heat flow from the dorsal fin, fluke blade, and flank are shown with SE bars. Numbers in parentheses indicate the number of trials at each activity level. Post-exercise dive values significantly less than post-exercise surface are indicated by *
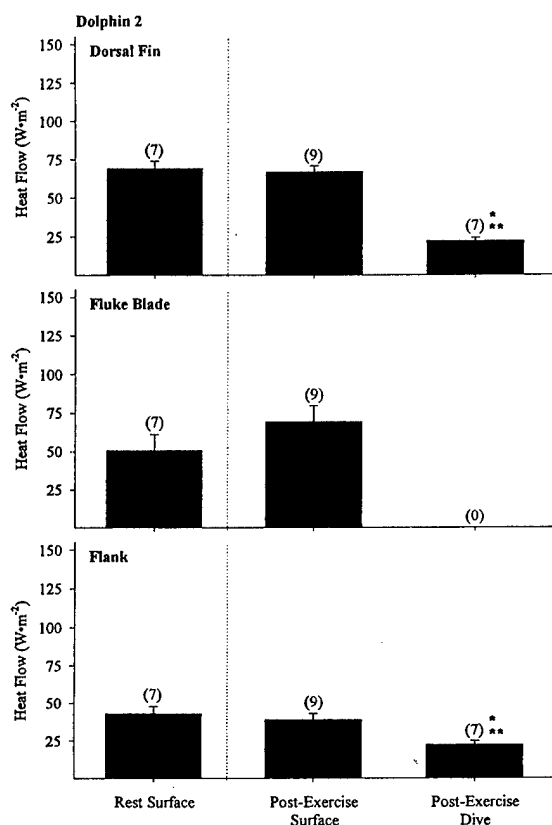
Fig. 5 Heat flow for three activity levels in dolphin 2. Post-exercise measurements at the surface and at 15 m depth were after 11–13 min of swimming at 4.3 m·s^{-1}. Mean heat flow from the dorsal fin, fluke blade, and flank are shown with SE bars. Numbers in parentheses indicate the number of trials at each activity level. Note that it was not possible to obtain fluke blade measurements on this animal during diving. Post-exercise dive values significantly less than post-exercise surface are indicated by *; post-exercise dive values significantly less than rest on the water surface are indicated by **
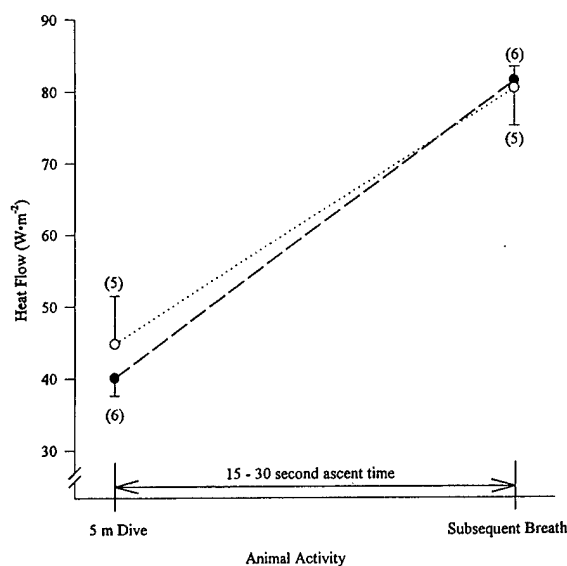

Fig. 6 Heat flow from the fluke blade (●) and dorsal fin (○) during a 5-m dive and subsequent breath. Numbers in parentheses designate the number of trials. Mean values are presented with SE bars in one direction only for clarity. *Dashed lines* connect the value at depth to the value during the breath for each measurement site, but they do not represent values measured between the two data points

the water surface (P < 0.05). The change in heat flow during a post-exercise dive was especially marked for dolphin 2 (Fig. 5). In addition to a reduction in heat flow from the dorsal fin, we found that heat flow from the flank of dolphin 2 was significantly less during a post-exercise dive than both rest and post-exercise at the water surface (P < 0.05) (Fig. 5).

Although the typical trend at depth was a reduction in heat flow, in one test, an unusually high measurement of 244.6 W·m^{-2} was obtained from the dorsal fin of dolphin 1 stationed at 15 m depth. In addition to the exercise period before the dive, this animal had completed multiple jumps out of the water immediately before the measurements were taken.

Temporal changes in heat flow

Mean heat flow during submergence to 5 m was 44.83 ± 6.65 W·m^{-2} for the dorsal fin and 40.10 ± 2.47 W·m^{-2} for the fluke blade of dolphin 3 (Fig. 6). During ascent, heat flow from the sites increased gradually, until the animal was 1 m below the water

surface. The maximum heat flow response occurred as the animal surfaced and breathed. Heat flow during the initial breath was significantly greater than the submerged value for the dorsal fin (t = -18.78, df = 4, P < 0.001) and fluke blade (t = -16.20, df = 5, P < 0.001). Mean values for heat flow from the dorsal fin increased by 79.3% while mean values from the fluke blade increased by 103.2% during the 15–30 s ascent.

Discussion

The typical mammalian response to exercise involves a redistribution of blood to the skin for enhanced heat transfer (reviewed in Brooks et al. 1996). In mammals adapted for aquatic living such as the bottlenose dolphin, this exercise response is complicated by the circulatory adjustments associated with diving. Bradycardia and decreased peripheral blood flow are important components of the dive response (Scholander 1940) but appear in direct conflict with the circulatory changes that occur with exercise. As a result, the active diving mammal must balance the peripheral circulation to accommodate thermoregulation that requires increased blood flow and oxygen conservation that demands decreased blood flow. In this study we find a hierarchy in the responses, with heat transfer from peripheral thermal windows being attenuated by the dive response in bottlenose dolphins.

The primary sites of heat loss in the bottlenose dolphin are the peripheral thermal windows located at the dorsal fin and flukes. During exercise, heat flow increases at these sites and remains elevated during recovery (Fig. 3). Similar results have been found for a

variety of cetacean species, including the harbor porpoise (Kanwisher and Sundnes 1965), the Hawaiian spinner dolphin (McGinnis et al. 1972; Hampton and Whittow 1976), and the Pacific (McGinnis et al. 1972) and Atlantic (Kanwisher and Sundnes 1966; Hampton et al. 1971) bottlenose dolphins.

Despite the high thermal conductivity of water, the dolphins in this study required a recovery period of at least 20 min to achieve resting heat flow values for all sites following swimming exercise. This recovery time is similar in duration to those reported for many terrestrial mammals exercising in air (Brown et al. 1993; Hodgson et al. 1993). Because heat transfer is 20–25 times faster in water than in air at comparable temperatures, the extended post-exercise recovery period for dolphins was not expected. However, several factors may have contributed to these results. First, the temperature differential between the water and core body was less than 8 °C in this study, resulting in a relatively small gradient for heat transfer. Second, the peripheral thermal windows represent only 30% of the total surface area of the Atlantic bottlenose dolphin (calculated from data in Hampton et al. 1971) which will limit the absolute heat loss from the body. Third, forced convective cooling, an important mechanism for increasing heat transfer during active swimming (Pabst et al. 1995), is reduced in sedentary animals during the recovery period. Therefore, the overall rate of heat dissipation may have been lower when the dolphins stopped swimming.

Heat transfer associated with exercise was also modified during diving. This was evident in the significant reductions in post-exercise heat flow during submergence when compared to post-exercise heat flow measured on the water surface (Figs. 4, 5). Although heart rate and blood flow were not measured in this study it is likely that cardiovascular changes associated with the dive response contributed to the observed reduction in heat flow (T.M. Williams, D.P. Noren, P. Berry, J.A. Estes, C. Allison, J. Kirtland, personal observation).

Like the dive response (e.g., Scholander 1963; Kooyman and Campbell 1972; Zapol et al. 1979; Hill et al. 1987; Kooyman 1989; Cherepanova et al. 1993; Guyton et al. 1995), thermoregulatory responses during submergence may not be an all-or-none phenomenon for marine mammals. The results from this study indicate that specific thermal demands alter the balance between diving and thermoregulatory responses. Previous studies on restrained harbor seals (Hammel et al. 1977) and ducks (Johansen 1964) show an override of the dive response during heat stress. Similarly, flexibility in the thermoregulatory response occurred during natural dives in the open ocean for the dolphins in the present study. Each of the dolphins showed variability in heat flow between the three measurement sites, with heat flow during a dive preferentially dissipated from the dorsal fin. There also appeared to be variability in heat dissipation strategies between the individual dolphins. For example, dolphin 2 showed significant reductions in post-exercise heat flow from the flank and dorsal fin

during a dive (Fig. 5). In comparison, dolphin 1 showed significant reductions in post-exercise heat flow only from the two peripheral sites during a dive; the flank remained unchanged (Fig. 4). For dolphin 2 heat flow levels during diving were significantly less than resting values. Dolphin 1 maintained heat flow above resting values when submerged, indicating an ability to partially reduce the thermal load during a dive.

The level of activity, and hence heat production, has an additional effect on heat transfer during submergence. The unusually high value of 244.6 $W \cdot m^{-2}$ from the dorsal fin of dolphin 1 at 15 m depth was obtained immediately after this animal had completed multiple jumps out of the water. Either a full dive response had not yet been initiated or the thermoregulatory responses of dolphins may be adjusted even during submergence. Such adjustments in the dive response to allow momentary increases in heat flow would allow a partial reduction in exercise-induced thermal loads without a complete override of the dive response and consequent increase in oxygen utilization (Gallivan and Ronald 1979).

We were unable to measure core body temperature in the current study. Other studies, however, have reported conflicting results regarding the effects of submergence on core body temperature. Reductions in core and aortic temperatures of freely diving pinnipeds at depth have been observed (Kooyman et al. 1980; Andrews et al. 1994) as well as temperature reductions at the water surface between dives (Hill et al. 1987). Harp seals diving in a pool showed no decrease in core temperatures with submergence (Gallivan and Ronald 1979). Another diving endotherm, the king penguin, shows marked regional heterothermy during diving (Handrich et al. 1997). Clearly, further investigation concerning the relationship between submergence and core temperature is needed for endothermic animals. In particular, the balance between peripheral heat flow and maintenance of a stable core temperature in diving cetaceans warrants further study.

An interesting result from the present study is the temporal change in heat transfer during ascent and the post-dive period. Significant increases in heat flow were measured from the dorsal fin and fluke blade upon the dolphin's first breath following a dive (Fig. 6). The thermal response associated with emergence from a dive parallels changes in heart rate for bottlenose dolphins (T.M. Williams, D.P. Noren, P. Berry, J.A. Estes, C. Allison, J. Kirtland, personal observation). Heart rate gradually increases in dolphins during ascent and is maximized when hyperventilation occurs upon emergence (Elsner et al. 1966). Although heart rate could not be monitored concurrently with heat flow in the present study, the temporal patterns suggest a link between cardiovascular and thermal events during and after a dive by dolphins.

In general, the thermoregulatory status of dolphins is dependent on activity level and state of submergence. During rest, there is minimal heat dissipation. Exercise on the water surface results in an increase in heat flow from all sites, with the largest changes occurring at the

thermal windows, the dorsal fins and fluke blades. Diving attenuates the exercise response and delays heat transfer to accommodate the dive response. The results of this study suggest that there is flexibility in the balance between these two apparently conflicting physiological responses. Under conditions of intense activity, and presumably high heat loads, heat transfer may increase momentarily during submergence. However, the majority of heat transfer usually occurs when the dolphin resurfaces, thereby preserving the oxygen-sparing benefits of the dive response.

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